Scientific Excellence • Resource Protection & Conservation • Benefits for Canadians
Excellence scientifique • Protection et conservation des ressources • Bénéfices aux Canadiens

Modelling the Coastal Migration of Juvenile Salmon Through Hecate Strait, British Columbia

M. C. Healey

Department of Fisheries and Oceans
Biological Sciences Branch
Pacific Biological Station
Nanaimo, British Columbia V9R 5K6

July 1989

Canadian Technical Report of Fisheries and Aquatic Sciences No. 1700

Fisheries and Oceans Pêches et Océans

Canada

Canadian Technical Report of Fisheries and Aquatic Sciences

Rapport technique canadien des sciences halieutiques et aquatiques

Canadian Technical Report of
Fisheries and Aquatic Sciences No. 1700

July 1989

MODELLING THE COASTAL MIGRATION OF JUVENILE SALMON THROUGH HECATE STRAIT, BRITISH COLUMBIA

by

M. C. Healey

Department of Fisheries and Oceans
Biological Sciences Branch
Pacific Biological Station
Nanaimo, British Columbia V9R 5K6

90-01931/

(c) Minister of Supply and Services Canada 1989

Cat. No. Fs 97-6/1700E ISSN 0706-6457

Correct citation for this publication:

Healey, M. C. 1989. Modelling the coastal migration of juvenile salmon through Hecate Strait, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1700: 97 p.

ABSTRACT

Healey, M. C. 1989. Modelling the coastal migration of juvenile salmon through Hecate Strait, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1700: 97 p.

In 1984 the Fisheries Research Branch of the Department of Fisheries and Oceans initiated a wide ranging study of the fish community of Hecate Strait. This report summarizes predictions of a model of juvenile salmon migration through Hecate Strait that was part of that study. The model predicts seasonal abundance, size, and food resource requirements of juvenile salmon in the Strait based on estimates of juvenile production in various regions of the coast, seasonal migration rates and timing, growth rates, mortality rates, and food conversion rates under different assumptions about the migratory routes followed by juveniles from different parts of the coast. Estimates of seasonal abundance, species composition, size, and food requirements of juveniles in Hecate Strait vary widely depending on the migration route of the juveniles. Sensitivity analysis of the principal uncertain parameters of the model showed that the qualitative patterns of seasonal abundance, size, etc., did not change with changes in the parameter values. The results suggest that sampling at particular times of year in Hecate Strait and comparing species composition, size, and changes in catch rate between sampling times would indicate the most likely patterns of juvenile salmon migration along the coast.

RESUME

Healey, M. C. 1989. Modelling the coastal migration of juvenile salmon through Hecate Strait, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1700: 97 p.

En 1984, la Direction de la recherche sur les pêches du ministère des Pêches et des Océans a entrepris une étude portant sur de nombreux aspects de la communauté de poissons de détroit d'Hécate. Le présent rapport résume les prévisions d'un modèle de migration des saumons juvéniles dans le détroit d'Hécate, utilisé dans le cadre de cette étude. Le modèle prédit l'abondance saisonnière, la taille et les exigences alimentaires des saumons juvéniles du détroit à partir d'estimations (production de juvéniles dans divers secteurs de la côte, taux de migrations saisonnières et dates, taux de croissance, taux de mortalité et taux d'assimiliation des aliments) en fonction de diverses hypothèses concernant les routes migratoires empruntées par les juvéniles provenant de divers secteurs de la côte. Les estimations de l'abondance saisonnière, de la composition par espèces, de la taille et des exigences alimentaires des juvéniles du détroit d'Hécate varient grandement en fonction de la route de migration des poissons. Une analyse de sensibilité des principaux paramètres imprécis du modèle a révélé que les distributions qualitatives de l'abondance saisonnière, de la taille, etc. ne variaient pas lorsque se modifiaient les valeurs des paramètres. Ces résultats semblent indiquer que l'échantillonnage à des moments précis de l'année dans le détroit d'Hécate permettant de comparer la composition par espèces, la taille et les variations du taux de captures selon les échantillonnages constituerait le meilleur indicateur des distributions de migrations des saumons juvéniles le long de la côte.

INTRODUCTION

In 1984 the Fisheries Research Branch of the Department of Fisheries and Oceans initiated a wide ranging study of the fish community of Hecate Strait, British Columbia (Fig. 1). The purpose of the study was to provide an ecological basis for multispecies management advice (Tyler 1986). The principal focus of the study was the commercially important groundfish species in Hecate Strait. Pelagic species were not ignored, however, and herring and salmon were important secondary foci.

When the program was initiated, a significant but unstudied component of the Hecate Strait fish fauna was the juveniles of Pacific salmon (Oncorhynchus) species. Each spring large numbers of five species of Pacific salmon leave their freshwater nurseries in rivers tributary to Hecate Strait and enter the Strait. How long these fish remained within the Strait, what benefits they derived from the Strait, and what impact they had upon the biotic community of the Strait were unknown in 1984. Also unknown was whether juveniles from the many river systems to the south of Hecate Strait passed through the Strait on their way to open ocean nursery areas. Historic sampling for juvenile salmon along the outer coast suggested that Hecate Strait might be such a migration corridor (Hartt and Dell 1986) but this was speculative.

In 1984, therefore, I began an investigation of the abundance, residency, and resource requirements of juvenile salmon in Hecate Strait. Although virtually no data on juvenile salmon were available from Hecate Strait itself, a number of studies had been conducted on the periphery of Hecate Strait and quite detailed studies of juvenile salmon abundance, growth, and dispersal existed for other parts of the Pacific coast (Healey 1967, 1978, 1980; Groot and Cooke 1987; Barraclough and Phillips 1978; Phillips and Barraclough 1978; Pearcy 1984; LeBrasseur and Barner 1964; Manzer 1956; Miller et al. 1982; Parker 1965, 1966; NOAA 1984). These studies provided a basis for speculation about the ecology of juvenile salmon in Hecate Strait.

Previous descriptions of juvenile salmon dispersal and abundance in the ocean have been based on extensive sampling to obtain information on seasonal and geographic trends in abundance and fish size. Such sampling is very demanding of physical and financial resources, particularly in a large body of water like Hecate Strait that is subject to frequent storms. Consequently, I approached the problem in a different way. Rather than beginning with an extensive fishing survey I first constructed a model of the coastal migration of juvenile salmon designed to calculate their seasonal abundance, size composition, and resource requirements in Hecate Strait. Output from the model identified critical times of sampling and measurements that would corroborate or contradict assumptions on which the output

depended. I then concentrated on sampling Hecate Strait during these critical periods rather than throughout the year.

In this report I describe the model and its predictions. Sampling during the critical periods and the interpretation of that sampling will be the subject of a subsequent report.

STRUCTURE OF THE MODEL

The problem is to predict the seasonal abundance and resource requirements of juvenile salmon in Hecate Strait. If only juveniles from rivers tributary to Hecate Strait are of concern, then such predictions may be made from knowledge of the time course and abundance of juveniles entering Hecate Strait from the tributaries, the average length of time that fish remain within Hecate Strait, and their feeding rate. If juveniles from elsewhere must be considered, then one must also know the time course of their arrival, their abundance, and so on. In constructing the model, therefore, I divided the coast into several compartments that would permit the model to reflect various feasible options with respect to juvenile migration through Hecate Strait (Fig. 2). For example, one option is that juveniles from rivers tributary to Hecate Strait and Queen Charlotte Sound migrate north through Hecate Strait, another that all juveniles from rivers to the south of Hecate Strait migrate north through the Strait. The model was designed to permit exploration of options such as these.

The Hecate Strait compartment, about which all model predictions were to be made, was the geographic area between a line drawn from Rose Spit to Edye Pass and a line drawn from Cape St. James to the south tip of Price Island (Fig 1). Other compartments were: 1) Central Coast, comprising the waters of Queen Charlotte Sound and adjacent mainland; 2) Northern Strait of Georgia, Johnston, and Queen Charlotte Straits; 3) Southern Strait of Georgia; 4) West Coast Vancouver Island; and 5) Dixon Entrance including the Nass and Skeena Rivers (Fig. 2).

A general assumption of the modelling was that the migration direction of juvenile salmon during their first ocean summer was north and west. The model does permit exploration of other options, such as that Nass and Skeena juveniles will dip down into Hecate Strait. I consider such options to be unlikely, however.

The model was designed to simulate, for each week, the average abundance, size, biomass, and food resource requirements of juvenile salmon in Hecate Strait on the basis of literature

values for such parameters as juvenile production rates, growth and migration rate. Some of the driving variables were fixed in the model and some could be varied interactively. The variables that could be varied interactively were: 1) the species; 2) the origin (coastal compartment) and migration route of juveniles destined to pass through Hecate Strait; 3) the number of juveniles of the chosen species that were produced in each compartment; 4) the size (fork length in mm) of juveniles at the time they began their migration toward Hecate Strait; 5) the week during which the juveniles in each compartment first began their migration; 6) the weekly growth rate (mm per week) of the juveniles in each compartment; 7) the weekly survival rate; and 8) the rate of migration in lengths per second. The fixed variables were: 1) the percent of juveniles initiating migration each week (initialized to a variable start week in 5 above); 2) the distance to be traveled from each coastal compartment to Hecate Strait (dependent on the migration route followed by the fish in 2 above); 3) the distance to be traveled through Hecate Strait; 4) the length to weight conversion for each species; and 5) the conversion efficiency of food into fish flesh.

Figure 3 is the flow diagram for the model and illustrates the process by which the outputs of weekly population size, fish size, biomass, and food requirements were calculated. The components of this process require further elaboration. The first submodel (Interactive Variable Selection, Fig. 4) prompts the operator either to accept the default values for migratory routes followed by the species and the driving variables over which he has control, or to change them.

In the second submodel (Calculation of Immigrant Numbers and Fork Lengths, Fig. 4) each coastal compartment and the various routes from that compartment to Hecate Strait are checked to determine whether fish from that compartment will migrate through Hecate Strait and the route they will follow in getting there. If fish were specified as traveling from a compartment to Hecate Strait the model calculated the time course (numbers per week) of their arrival in Hecate Strait and their size on arrival from the time course over which they initiated migration, the distance they traveled to reach Hecate Strait, their mortality rate, and their growth rate. These calculated numbers constituted a matrix of the weekly immigrant numbers and immigrant sizes to Hecate Strait.

In the third submodel (Population and Size Simulation, Fig. 5) the population of juvenile salmon and the mean size of the fish is calculated for Hecate Strait. This submodel steps through each week of the year and, for each week, checks the matrix of weekly immigrant numbers to see if any fish were to arrive in Hecate Strait that week. If there were immigrants they were added to the current population and a new mean length was calculated for the population as the weighted average of resident

and immigrant lengths. The population was then reduced by the weekly mortality rate and by emigration. Each weekly cohort of immigrants to Hecate Strait has a finite residence in the Strait determined by its speed of migration and the distance through the Strait. Emigrants were not, therefore, a random selection of the current population but were those fish that had been resident sufficiently long to have moved through the Hecate Strait compartment. Emigrants were, therefore, larger than the population mean size and the population mean size was adjusted following each emigration. Finally, the remaining fish in Hecate Strait were grown by the amount specified in the original variable selection. The estimates of weekly population size and fish length were then printed and the submodel moved on to the next week.

In the fourth submodel (Biomass and Food Requirements, Fig. 6) the biomass and food requirements of juvenile salmon in Hecate Strait are calculated and printed out. The mean weight of fish in Hecate Strait was first calculated from the species specific weight to length relationship taken from Healey (1980) and the estimated length of the fish in Hecate Strait from submodel 3. Biomass was the product of fish weight and estimated population from submodel 3. New biomass generated during the week was calculated from the weekly biomass estimate and the growth rate of the fish. A food conversion efficiency of 25% was assumed, so that the biomass of food required each week was 4X the new biomass of fish generated during the week.

MODEL VARIABLES

Juvenile Production by Coastal Compartment

I estimated the number of juvenile salmon produced within each coastal compartment from average species escapements for the decade 1973-1982 (Table 1). The time period was arbitrary, the objective being only to use escapement values that were realistic for each compartment. I used the arithmetic average of the recorded escapements during this period except for pink salmon, for which I calculated separate averages for even and odd year brood lines.

Escapement values were translated into estimates of juvenile production by means of constant multipliers for the average fecundity per female, the proportion female in the escapement, any presumed bias in the escapement estimate, and freshwater and coastal survival of juveniles up to the time that they begin their northward migration along the coast. These

multipliers were derived from various sources such as Healey (1986), conversations with colleagues, and personal experience. The uncertainty associated with each of the parameters used to estimate juvenile production is large, and the values cannot be considered to be better than informed guesses. Nevertheless, some initial set of such values is needed before the consequences of various migratory options can be investigated. The values in Table 1 are a first attempt at such an initial set.

For sockeye (O. nerka), I assumed that the escapement estimates were unbiased, that the average fecundity was 3400 (Manzer and Miki 1984), and that the sex ratio in the escapement was 1.0. Literature values suggest freshwater survival (egg to smolt) between 0.3 and 4.0% and coastal marine survival for the first month of between 12 and 71% (Healey 1986). A freshwater survival average of 2% and a coastal marine survival average of 40% seems reasonable, therefore. The problem is in combining these to obtain a total survival up to the time that the smolts begin their northward migration in the sea. Data from Fraser River sockeye in the Strait of Georgia suggest that these fish do not linger near the river mouth after downstream migration, but quickly begin their northward migration (Groot and Cooke 1987). The period of marine mortality prior to northward migration may be short for this species but, nevertheless, a high proportion of the coastal marine mortality may take place during the first few days of ocean life. A total freshwater and early marine survival of 0.8% seems too low, therefore, and of 2.0% seems too high. I arbitrarily chose the average of these (1.4%).

For pink (O. gorbuscha), I assumed that the escapement estimates were unbiased, that the average fecundity was 2000 for the odd year brood line and 1500 for the even year brood line, and that the sex ratio in the escapement was 1.0. An egg to emergent fry survival of 10% appears reasonable for pink salmon (Healey 1986; Hunter 1959), and Parker (1966) estimated that the survival of fry during their residence in nearshore waters was on the order of 30%. Thus, total survival from egg to the time at which the juveniles initiate their northward migration is about 3%.

For chum (O. keta), I assumed that the escapement estimates were unbiased, that the average fecundity was 3000, that the sex ratio in the escapement was 1.0, and that freshwater and coastal survival was the same as pink salmon.

For coho (O. kisutch), I assumed that the escapement was greatly underestimated. The extent of the bias is unknown, so I have arbitrarily doubled the escapement. Twice the recorded escapement may still underestimate the true escapement, however. Coho sex ratio I assumed to be 1.0, their fecundity 3500, and their freshwater and coastal survival the same as sockeye, 1.4%.

For chinook (O. tshawytscha), I also assumed that the recorded escapement was about 1/2 the true escapement (Healey 1982 and unpub. data). I further assumed that chinook sex ratio was 1.0 and their fecundity was 5000. It is extremely difficult to assign a value for freshwater and coastal mortality to chinook because of their complex life history. Most British Columbian stocks migrate to sea as underyearlings but remain in estuarine and coastal waters for some time. They, thus, have a longer freshwater and coastal residence than pink and chum but shorter than coho and sockeye. I arbitrarily set their freshwater and coastal survival at 2.5%.

From the point of view of interpreting predictions of my migration model there are two points of concern about the estimates of juvenile production in Table 1. These are the absolute and relative (among species) accuracy of the estimates. The absolute estimates could be in error by 100% or more because of assumptions I have made. For example, it is unlikely that escapement estimates are unbiased, as I have assumed for most species. Most likely the estimates are less than the true escapement. Also, it is unlikely that the sex ratio in the escapement is 1.0. Males outnumber females in many populations. The probable errors introduced by these assumptions work in opposition, however. Perhaps most serious are the great uncertainties in the estimates of freshwater and coastal survival. A small error in these estimates can greatly effect the estimate of absolute abundance. The relative abundance of the various species is, however, probably reasonably well captured by the estimates in Table 1.

Mean Size at Initiation of Northward Migration and Growth Rate

The mean size of each species at the time of initiation of northward migration and growth rate during the first ocean summer were taken mainly from data gathered in the Strait of Georgia (Healey 1980). Since there was little information on fish size and growth from other parts of the coast, the same starting values were assigned to each compartment. These were as follows:

Species	Fork Length mm	Growth mm/wk
Sockeye	100	4.20
Pink	70	7.00
Chum	75	5.25
Coho	100	7.00
Chinook	80	6.00

Information from other parts of the coast indicates considerable variability in size of juveniles among stocks, but also that the values for fork length at the start of northward migration are not unreasonable when the size of downstream migrant smolts and juveniles captured at sea early in the summer is considered (Wakefield et al. 1981; Parker 1965; Foerster 1968; Holtby and Hartman 1982; Healey 1982, unpub. data). The initial size estimates are relatively less critical than the growth rate estimates once the fish have been at sea for a number of weeks.

Growth rate estimates are much more difficult to obtain than mean size. There appear to be no reliable estimates of growth during early sea life. The estimates in Table 1 are based on changes in size with time within a geographic area, and these are probably biased low (Healey 1982). Hartt and Dell (1986) estimated rates of growth for sockeye and pink salmon during their first ocean summer that were considerably greater than those used above (7-12.6 mm/wk for sockeye and 12.6-13.3 mm/wk for pink). However, these estimates were based on a few fish that were well offshore and a considerable distance from their natal river when first captured. They may, therefore, have been among the faster growing members of the year class. A growth rate of almost 2 mm/d for pink salmon during their first weeks at sea seems unreasonably large. On the other hand, incremental increase in length may not be constant over the summer but may increase as the fish get bigger. Growth rate may also vary among stocks and regions, although Hartt and Dell (1986) found the same growth rate for Fraser and Skeena River sockeye salmon. Recent observations by Fisher and Pearcy (1988) suggest growth rates for juvenile coho off Oregon and Washington that ranged 4.8-11.8 (mean, 8.0) mm/wk, or somewhat larger than the estimate of 7 mm/wk that I used. The effects of different assumptions about growth rate on predictions of the model will be tested.

The Timing and Speed of Northward Migration

The same basic pattern of migratory behaviour is assumed for each coastal compartment and is as follows: Juveniles of each species arrive in the ocean over a period of several weeks reflecting the time dependent pattern of their downstream migration. Each group of fish arriving at the rivermouth may delay for a period of a few hours to several weeks (depending on the species) in the vicinity of the natal river mouth before initiating northward migration. The initiation of northward migration following this delay at the river mouth is assumed to have the same time dependent pattern as the downstream migration. Once a group of fish has begun northward migration it is assumed to continue migrating at a constant rate relative to its size (i.e. X-lengths-per-second) until it has moved through Hecate Strait. Migratory behaviour in the model is, therefore, characterized by a week during which northward migration begins,

a set of values specifying what proportion of the juvenile production begins migration during the weeks following the initiation of northward migration, and a rate of travel in lengths-per-second. Only the start week and rate of travel can be user specified in the model.

For all species I assumed that northward migration was initiated somewhat later in the more northern coastal compartments. Start weeks for each species by coastal compartment were as follows (for reference, week 18 is the first week of May and week 25 is the fourth week of June):

	Compartment					
Species	South Geo. Str.	North Geo. Str.	West Cst. Van. Isl.	Central Coast	Hecate Strait	Dixon Entr.
Sockeye	18	18	18	19	20	20
Pink (o)	17	17	17	18	19	19
Pink (e)	17	17	17	18	19	19
Chum	18	18	18	19	20	20
Coho	17	17	17	18	19	19
Chinook	25	25	25	26	27	27

The weeks of initiation of migration shown above are based mainly on downstream run timing from river smolt and fry trapping studies but also partly on early sea life studies. For sockeye the main period of downstream migration on the southern part of the B.C. coast appears to be from mid April to mid May with a peak in the last week of April or the first week of May (Hyatt et al. 1984; Foerster 1968). Groot and Cooke (1987) noted that sockeye first become abundant off the Fraser River mouth in the last two weeks of April. On the central coast the timing of downstream run is later, from late April to late May, and on the north coast later still, from mid May to late June (Hyatt et al. 1984; Brett and McConnell 1950; Johnson and Groot 1963). Since sockeye appear to have a relatively brief delay at the river mouth before initiating their northward migration, start weeks were chosen to reflect the downstream run timing.

Examples of downstream run timing for pink and chum salmon are given in Randall et al. (1987), Healey (1979), Hunter (1959), and Bailey (1979). The Strait of Georgia region is dominated by odd brood year pink runs (even year fry) from the Fraser which normally extend from late February through until the end of May with a median early in the 4th week of April. Pink fry runs on the central coast extend from early April to late May with a median late in the 4th week of April. Chum fry have a similar run timing but the median tends to be a few days later than pink. Both these species linger in the vicinity of their

natal river for 3 to 4 weeks before beginning northward migration. The start weeks for these species reflect this delay.

Coho appear to have a similar downstream run timing to sockeye, with peak migration occurring in early May on the south coast and somewhat later further north (Holtby and Hartman 1982; Lister and Walker 1966; Hunter 1959). Coho also disperse rapidly from their natal river mouth (Healey 1982), however, the time at which they actually begin northward migration is in doubt. The start weeks shown above are, therefore, somewhat arbitrary.

Chinook have a variable juvenile life history with seaward migration occurring at a variety of times and ages (Healey 1980; Carl and Healey 1984). In British Columbia the majority of chinook either migrate immediately to the river estuary on emergence as fry, where they reside until early June, or they migrate in June as fingerling smolts. Chinook smolts, thus, appear to begin their northward dispersal in early June.

The values specifying what proportion of the juvenile production begins migration during the weeks following the initiation of northward migration were estimated from downstream run data for each species, and assuming a normal distribution of these proportions. The specific distributions used are shown in Fig 7. For sockeye, coho, and chinook the distribution spans 8 weeks following the initiation of migration whereas for chum and pink the distribution spans 11 weeks.

Rate of migration is another value for which there is very little information. Groot and Cooke (1987) estimated that sockeye smolts in the Strait of Georgia migrated an average distance of 6-7 km/day. Assuming the smolts were about 10 cm long, this suggests an average speed of 0.7-0.8 lengths/second. Information in Healey (1967) and Parker (1965) indicates that pink salmon fry took between 20 and 30 days to migrate about 70 km down Burke Channel in central British Columbia. Assuming the fry averaged between 4.5 and 5.0 cm during this stage of their life, their migration rate was between 0.6 and 0.8 length/second, similar to sockeye. Information in Hartt and Dell (1986), however, indicates that larger fish may move considerably faster than these rates, suggesting that migration may speed up as the fish get larger. Consequently, I used 1 length/second as the default value for migration rate for sockeye, pink, and chum salmon, but tested values ranging from 0.5 to 1.5 lengths/second.

Migration rates for coho and chinook are probably considerably slower as the movement of these fish appears to be more a gradual dispersal than a directed migration. I arbitrarily chose migration rates of 0.1 lengths/second for these species.

Natural Mortality Rates

Mortality rates during the first few months at sea are unknown. Estimates in the literature, based mainly on the assumption that mortality is proportional to weight, are summarized by Ricker (1976). These suggest an average weekly survival for sockeye during the first 6 months of ocean life of about 97%. I have used this value for sockeye, coho, and chinook. On the assumption that pink and chum suffer higher ocean mortality because of their smaller size I have assumed a weekly survival for these species of 91%. I explored the sensitivity of model predictions to a range of survival rates.

RESULTS

GENERAL FEATURES OF MODEL OUTPUT

Variation in juvenile production by species among coastal compartments (Table 1) suggests that different assumptions about the migratory route of juveniles should result in different relative abundances of the species of salmon in Hecate Strait. Also, since the juveniles from the various coastal compartments should, to some degree, move sequentially through Hecate Strait, the species composition in the Strait should change seasonally. These expectations should be reflected in the model output.

Some characteristics of model output for extreme assumptions about migratory behaviour are shown in Table 2. The minimal assumption is that only young salmon from rivers tributary to Hecate Strait migrate through the Strait. Under this assumption, sockeye are present in the strait for 8 weeks, pink and chum for 12 weeks, and coho and chinook for 14 weeks. All species reach peak abundance about half way through their period of residence. Juvenile salmon, thus, appear in the Strait in late May, are most abundant in late June or early July, and are gone by early August, except for chinook which are predicted to be about 7-8 weeks later than the other species. Peak numbers ranged from about 650,000 for sockeye to more than 21 million for even brood year (odd calendar year) pink salmon. Maximum size achieved ranged from 84 mm for pink salmon to 149 mm for coho, and food resources consumed ranged from 16.5 metric tons for sockeye to 774.1 metric tons for even brood year pink salmon (Table 2).

The maximal assumption about migratory behaviour was that all juvenile salmon from coastal compartments south of Hecate Strait migrate north through Hecate Strait. There are two forms of this assumption. One in which the young fish from southern Strait of Georgia migrate north through Johnstone and Queen Charlotte Straits on the east side of Vancouver Island, and a second in which these young fish migrate north through Juan de Fuca Strait and along the west side of Vancouver Island. The results for the former route are shown in Table 2, as this appears to be the most likely route of juveniles from southern Strait of Georgia. If the fish were to follow the route up the west side of Vancouver Island, the length of time during which juvenile salmon were present in Hecate Strait would be lengthened slightly and the maximum numbers reduced slightly for some species, but the basic pattern would not alter.

Under the assumption that all juveniles migrate north through Hecate Strait, the period during which young salmon were present in the Strait was lengthened considerably, to 16 weeks for sockeye, 20 weeks for pink, 21 weeks for chum, and the full year for coho and chinook. The time of peak abundance was also considerably later in the year for sockeye, odd brood year pink, chum, and chinook but not for even brood year pink and coho. These results reflect the relative production of juveniles among coastal compartments and the time it takes for production from each compartment to reach Hecate Strait. Chum, sockeye, odd brood year pinks, and chinook, for example, are very abundant in the southern Strait of Georgia compartment and create the late peak in numbers in Hecate Strait when they pass through. Even brood year pinks, on the other hand, are abundant in the Hecate, Central Coast, and Northern Strait of Georgia compartments, so that in odd numbered years pinks reach peak abundance early in the year in Hecate Strait. Coho, although produced in high numbers in south coast compartments, have a slow rate of northward dispersal. High production from regions to the south of Hecate Strait is sufficiently reduced by natural mortality before reaching the Strait that local production generates the local peak in abundance.

The peak abundance of sockeye, pink, and chum was greater (18 - 36 million at the peak) and average size of all young salmon was greater (ranging from 143.2 mm for chum to 321.4 mm for coho) in Hecate Strait when juveniles from the south moved through the Strait. Food resources utilized were also much larger, up to 2 orders of magnitude larger in the case of sockeye (Table 2).

SEASONAL PATTERNS OF ABUNDANCE UNDER DIFFERENT MIGRATORY ROUTE ASSUMPTIONS

Abundance curves for the five species (separate curves for even and odd brood year pink salmon) under the assumptions that only juveniles from tributaries of Hecate Strait migrate through the Strait or that all juveniles from southern compartments migrate north through the Strait are shown in Figures 8-13. For sockeye and chum, two intermediate assumptions (1. juveniles from the Central Coast and Hecate Strait move north through the Strait; 2. juveniles from Northern Strait of Georgia, Central Coast, and Hecate Strait migrate north through the Strait) are also shown. For pink salmon the alternative that juveniles from the Southern Strait of Georgia migrate north via Juan de Fuca Strait and the West Coast of Vancouver Island is also shown.

As indicated in Table 2, the assumption that juveniles from all coastal compartments to the south migrate north through Hecate Strait lengthened the period of time during which juvenile salmon were abundant in Hecate Strait and, except for coho, increased the peak abundance of juvenile salmon in Hecate Strait (Figs. 8-13). For sockeye, pink, and chum salmon the predicted length of time that juveniles are abundant in Hecate Strait and the maximum population size increased progressively as juveniles from more southern compartments were routed through the Strait. This progression is illustrated for sockeye and chum in Figures 8 and 11, which show that the seasonal patterns of abundance of sockeye and chum for the intermediate assumptions about migratory routes of juveniles were intermediate between the extreme assumptions.

Both odd and even brood year pink salmon showed seasonal patterns of abundance similar to chum salmon, although even brood year pink salmon were considerably more abundant in the spring than either odd brood year pink salmon or chum salmon. Both brood lines of pink showed a long flat peak of abundance extending from late May until late September when all juveniles from compartments to the south migrated north through Hecate Strait (Figs. 9, 10). Routing Southern Strait of Georgia juveniles via the West Coast of Vancouver Island lengthened the period during which pinks were abundant in Hecate Strait by about 2 weeks during even numbered years, but did not greatly change the absolute abundance or seasonal pattern of abundance compared with the assumption that all Strait of Georgia juveniles moved north through Johnstone and Queen Charlotte Straits (Figs. 9-10). In odd numbered years there are no pink salmon juveniles produced in the southern Strait of Georgia so that the route followed by pinks from this compartment was not relevant. The result of routing sockeye and chum salmon from southern Strait of Georgia

via the west coast of Vancouver Island was similar to that for odd brood year pink salmon.

Coho and, particularly, chinook were much less abundant than the other species. The model predicted that each species would be abundant for a few weeks if only Hecate Strait tributaries contributed to the Hecate Strait population but that both species would remain abundant from mid summer to the end of the year if coastal regions to the south also contributed juveniles to the Strait (Figs 12-13). However, the model probably does not capture the behaviour of coho and chinook very well. My expectation for these species is that they would be relatively rare in Hecate Strait in summer compared with the other species, but that they should continue to be present after the other species have left.

The picture that emerges from these predictions is that, if only juveniles from tributaries of Hecate Strait utilized the Strait, there would be a relatively brief, 6-12 week, period in spring and early summer during which juvenile salmon were abundant in Hecate Strait. If juveniles from all regions to the south of the Strait migrated north through the Strait, however, there would be a protracted, 14-20 week, period lasting from May through September during which juvenile salmon, particularly sockeye, pink, and chum, were abundant in Hecate Strait.

The increase in predicted abundance of sockeye in Hecate Strait when all juveniles from the south migrate through the strait is dramatic, almost 2 orders of magnitude. Sockeye should, therefore, be measureably more abundant in Hecate Strait in late summer than in early summer if they display such migratory behaviour. The increase was less dramatic for pink and chum, about 2X. Odd brood year pink and chum had long flat peaks of abundance whereas even brood year pink and sockeye had more well defined peaks (Figs 8-11). Thus, odd brood year pink and chum should not be dramatically more abundant late in the summer, but should maintain their abundance as juveniles from more southern compartments migrate into Hecate Strait to replace those leaving the Strait by Dixon Entrance (Figs 9-11). Even brood year pink, on the other hand, should decline in abundance throughout the summer. Coho and chinook salmon were predicted to change little in abundance through the summer and autumn (Figs 12, 13).

PERCENT COMPOSITION OF THE JUVENILE POPULATION IN HECATE STRAIT

The predicted percent composition of the juvenile population in Hecate Strait in even years is shown in Figures 14-18 for the extreme assumptions about juvenile migratory behaviour. Sockeye contribute only about 5% to the juvenile population if only local juveniles utilize the Strait, but contribute about 45% in late July if all juveniles from the south move through Hecate Strait (Fig. 14). The contribution of odd brood year pink salmon was high early in the spring but declined steadily as the season progressed (Fig. 15). If only Hecate Strait tributaries contributed to the population, the percent of pink salmon in the Hecate Strait juvenile population declined to an insignificant amount by mid August, whereas if juveniles from the south migrated north through the Strait the percentage of pink salmon remained between 20 and 30% until late September (Fig. 15). Chum salmon showed a single peak in percentage contribution of about 45% in early July if only Hecate tributaries contributed to the Hecate Strait population but showed two peaks in contribution (about 34% in late June and about 58% in mid August) if juveniles from the south migrated through the Strait (Fig. 16). If only local coho used Hecate Strait the model predicted that they would constitute between 20 and 40% of the population from May through July (Fig. 17). If coho from the south migrated north through Hecate Strait, however, the percentage of coho dropped from about 30% in late May to almost nothing by mid August, rose quickly to over 80% about mid October, dropped to 34% at the end of November, then rose to 87% at the end of the year. The model predicted that chinook would constitute a high proportion of the local population in the fall and winter if only local stocks contributed to the population, but a smaller percentage if stocks from further south migrated into Hecate Strait (Fig. 18). Under the latter assumption the model predicted a peak in the percentage of chinook during November which coincided with a dip in contribution by coho at this time. This pattern occurs because, by this time of year, coho and chinook are the only salmon species in Hecate Strait.

As expected from the differences in production by species in the different regions of the coast, the predicted composition of the population in Hecate Strait was dependent on the assumptions about which regions of the coast contributed juveniles to the Hecate Strait population. Thus, it appears that the composition of the juvenile population in the Strait, particularly the composition during July and August, should be indicative of whether juveniles from southern areas migrate north through Hecate Strait (Table 3). Most important from the point of view of attempting to apply the model, it should be possible to distinguish between a delayed movement of local juveniles (if,

for example, the migratory timing variables I have chosen are incorrect) and the arrival of juveniles from further south.

Because of the differences in pink salmon production between odd and even year brood lines, the percentage composition estimates from the model differ between even and odd numbered years (Table 3). The only large differences are in the contribution of pink and chum salmon to the Hecate Strait population when juveniles from southern B.C. migrate north through Hecate Strait. Pink juveniles of the even year brood line are more abundant, but their production is also concentrated further north. Thus, the contribution of pinks to the Hecate Strait population during odd numbered years is considerably higher than during even numbered years throughout most of the summer (Fig. 19). In the late summer, however, the odd year brood line contributes more because of the influx of Fraser River juveniles so that, in even years, pinks remain a major component of the juvenile population well into September. The chum salmon contribution is correspondingly lower early in the season in odd numbered years, but higher later in the season (Fig. 20).

THE SEASONAL PATTERN OF AVERAGE LENGTH FOR EACH SPECIES

If only juveniles from streams tributary to Hecate Strait contributed to the population in the Strait the predicted increase in average size of fish in the Strait over time was relatively small for all species (Figs. 21-24). This is because, although weekly growth rates were quite high, new, small, fish were being recruited from local streams during most of the period that juveniles were present in the Strait and because emigration from the Strait was biased toward the larger fish. When juveniles from coastal compartments to the south migrated through Hecate Strait, however, the average size of juveniles in the Strait increased dramatically during June, July, and August (Figs 21-24). This is because large juveniles were being recruited to the Hecate Strait population from the compartments to the south. As was the case with seasonal patterns of abundance, intermediate assumptions about which juveniles migrated north through Hecate Strait produced intermediate patterns of increasing length (Figs 21, 23). If juveniles from southern Strait of Georgia were routed via Juan de Fuca Strait and the West Coast of Vancouver Island then the rapid increase in average size in Hecate Strait was delayed, but the final size of juveniles was larger than if they had migrated via Johnstone and Queen Charlotte Straits (Fig. 22).

Sockeye were predicted to be 30% longer in mid July if juveniles from the south migrated through Hecate Strait, pink 38% longer, and chum about 30% longer. These represent absolute

differences of about 30 mm for all three species, a difference that should be easily detectable from field samples. Coho and chinook also show an increase in average size associated with the addition of juveniles from southern compartments, but the increase occurs considerably later in the season because of the much slower rate of northward dispersal assumed for these species (Fig. 24).

FOOD RESOURCE DEMANDS BY JUVENILE SALMON IN HECATE STRAIT

Table 4 and Figures 25-27 summarize the predicted food resource requirements of juvenile salmon during their residence in Hecate Strait under different assumptions about migration routes. The resource requirements under the assumption that only juveniles from rivers tributary to Hecate Strait utilize the Strait are relatively modest, generally less than 50 tons for any species in any week, except even year brood line pink salmon, which required over 100 tons for most of June and coho which required between 50 and 100 tons during most of June and July (Figs 25-27). The greatest food requirements for all species were during June and July except for chinook for which the greatest requirement was in August and September.

At the other extreme, the maximum food resource requirement under the assumption that all juveniles from the south migrated north through Hecate Strait often exceeded 200 tons per week and, in the case of odd year brood line pink, went as high as 450 tons per week (Fig 25-27). The timing of maximum food demand was also shifted later, to the end of July and beginning of August for sockeye, mid to late August for odd year brood line pink salmon, June and July for even year brood line pink salmon, end of August and early September for chum, and into the winter for coho and chinook (Figs 25-27).

If an intermediate migration route assumption was made the food resource requirements were also intermediate between the extremes and the timing of maximum requirement was not pushed back so far in time (Table 4). When southern Strait of Georgia salmon were routed via Juan de Fuca Strait and the West Coast of Vancouver Island the total food requirement in Hecate Strait was generally lower than when these juveniles migrate by the shorter route through Johnstone and Queen Charlotte Straits.

MODEL SENSITIVITY TO VARIATION IN SELECTED PARAMETERS

I examined the sensitivity of model output to variation in weekly survival rate, weekly growth rate, and migration rate.

Reducing survival, logically, reduces the number of salmon expected in Hecate Strait. The effect is greatest on those arriving from the most southerly coastal areas because these suffer the greatest time lag between leaving their home compartment and arriving in Hecate Strait. Reducing sockeye weekly survival from 0.97 to 0.9 and 0.85 reduced peak abundance of this species in Hecate Strait from 29 million to 14 million and 8.7 million respectively. At a weekly survival rate of 0.85 the obvious peak in abundance late in the season corresponding to the arrival of Fraser River sockeye was not apparent (Fig. 28). Reducing odd brood year pink salmon weekly survival from 0.91 to 0.85 and 0.8 reduced the peak abundance of this species in Hecate Strait from 18 million to 9.7 million and 7.8 million respectively. As with sockeye, the peak in numbers shown late in the season at the higher survival rate (again due to juveniles from the Fraser River) was reduced at the lower survival rates. In fact, at a weekly survival of 0.8, odd brood year pink numbers peaked in June rather than August (Fig. 29).

The effect of changing survival on chum salmon numbers was similar to the effect on sockeye and pink salmon.

The reduced numbers under lowered survival rates also resulted in a slightly smaller average size of each species (because fewer large fish were arriving from the south) and in considerably lower biomass and food resource requirements (because of the smaller numbers and smaller physical size of the fish).

Increasing the weekly growth rate of sockeye from 4.2 to 7 mm and of odd brood year pink from 7 to 8.4 mm resulted in substantially increased average size of fish in Hecate Strait when all juveniles from the south were assumed to move through the Strait. When only Hecate Strait juveniles moved through the Strait the effect of increasing growth rate was small (Figs. 30, 31). With the faster growth rates went more rapid rates of travel so that, if the increase in growth was great enough, juveniles were present in the strait for a shorter time. As a consequence, peak numbers in the Strait were sometimes lower when growth rates were faster, but peak biomass and food resource requirements were considerably larger owing to the larger size of the individual fish and their faster growth rate (Table 5).

If only juveniles from Hecate Strait tributaries were assumed to migrate through the Strait then changing the migration rate had profound effects on the estimated abundance, biomass,

and food requirement, as illustrated by sockeye and odd brood year pink salmon (Fig. 32). Comparing migration rates of 0.5 and 1.5 lengths per second (lps) shows that residence time was shortened by 2-3 weeks, and peak numbers reduced by about 40% (Fig. 32). Peak biomass was also reduced by 45-65%, and food requirement by 50-65% at the higher migration rate.

If all juveniles from the south were assumed to migrate through Hecate Strait then increasing the migration rate to 1.5 lps shortened the residence time of juveniles in Hecate Strait by about 3 weeks and pushed the time of peak abundance earlier in the season (Figs. 33 and 34). Reducing the migration rate to 0.5 lps greatly increased residence time of juveniles in Hecate Strait and, in general, stretched out the period of high abundance in the Strait by 7-9 weeks (Figs. 33 and 34).

Peak numbers expected in the Strait were not greatly affected by a change in migration rate if all juveniles from the south migrated through the Strait. Biomass and food resource requirements, however, were changed. In the case of sockeye, estimated food requirements were in excess of 4200 tons at a migration rate of 0.5 lps, whereas they were less than 1600 tons at a migration rate of 1.5 lps. Similarly, for odd brood year pink salmon, estimated food requirements were 4500 tons and 2270 tons at migration rates of 0.5 and 1.5 lps.

Thus, some basic features of the model output are quite sensitive to assumptions about the rates of mortality, growth, and migration. Precise quantitative prediction of abundance, size, and food requirements for any species is, therefore, unlikely to be successful. From the perspective of comparing among assumptions about migration routes of juveniles, however, predictions are possible. If all fish from the south migrate through the Strait, the model predicts high abundance of comparatively large pink, sockeye, and chum into late summer at all reasonable values of survival, growth, and migration rate but virtual absence and relatively small size of these species if only Hecate Strait juveniles use the Strait.

DISCUSSION

It is certain that some juvenile salmon migrate through and extract resources from Hecate Strait during their first summer at sea. What is in question is how many of each species migrate through the Strait, how long each species is present, and how much in the way of food resources are obtained from Hecate

Strait. Preliminary answers to these questions are provided by the model described in this report.

The model assumes that the answers to the questions posed depend primarily on the number of juveniles that migrate seaward from rivers tributary to various regions of the coast, whether their migration route into the north Pacific carries them through Hecate Strait, and their rates of migration, growth, and survival. The number of key parameters and the uncertainty about their values are sufficiently large that a virtually infinite number of plausible patterns of abundance, size, and food resource requirements could be calculated for Hecate Strait. To reduce the possibilities to a manageable number I made the following restrictive assumptions:

1. Once they have begun migrating north, salmon from all parts of the coast move continuously at the same relative rate but the rate for coho and chinook is different from that for pink, chum, and sockeye.

2. Each species, regardless of its area of origin, enters the ocean at the same size and experiences the same rate of growth and mortality but these rates differ among the species.

3. All fish from a particular region of the coast follow the same migration route to the north Pacific Ocean.

Even when constrained by these assumptions the model still provided a rich variety of patterns of abundance, size, and resource requirements of juvenile salmon in Hecate Strait when the migratory routes followed by juvenile salmon to the north Pacific Ocean were varied. The predicted patterns of abundance and size of juvenile salmon in Hecate Strait associated with different assumptions about juvenile migratory routes were quite route specific. Midsummer species and size composition of juvenile salmon in Hecate Strait and changes in relative abundance during July and August may, therefore, be diagnostic for the coastal migration routes followed by juveniles. This is provided the key features of the migration are captured by the model.

Apart from species composition changes, which were dependent on the distribution of spawning activity by the various species along the coast, the length of time during which young salmon were present in Hecate Strait, their maximum abundance in the Strait, and the food resource demands they made on the Strait all increased as more coastal areas to the south were added to the list of those contributing to the population in Hecate Strait. The timing of peak abundance and of peak food resource demands also tended to be later in the year when juveniles from southern compartments migrated north through Hecate Strait. For Hecate Strait to provide a rich feeding ground for juveniles from

southern Strait of Georgia as well as from local tributaries, high plankton production in the Strait would have to extend throughout the spring and summer months.

In my view the model is likely to capture the migratory behaviour of sockeye, pink, and chum salmon reasonably well. It is much less likely to capture the migratory behaviour of coho and chinook. These latter two species make a relatively minor contribution to numbers in Hecate Strait. However, because of their large size and slow dispersal rate they make substantial food resource demands on the Strait. By mid to late summer, however, these species should have switched substantially to a fish rather than a plankton diet (Healey 1980), whereas pink, chum and sockeye should continue to depend on plankton production.

The principal limitation of the model with respect to coho and chinook is the assumption of continuous northward migration. In my view the dispersal of these species is much less directed and much less continuous than it is for the other three species. The principal oceanic habitat of coho and chinook is continental shelf waters (Healey 1983 and unpub. data) so that they have effectively completed their migration once they abandon the estuary of their natal river. I have attempted to simulate the more casual dispersal of these species by means of a slow migration rate. However, I am not statisfied that this has been successful.

Assuming that the model has successfully captured the coastal migration of sockeye, pink, and chum, it is worth while to examine the diagnostic features of summer species composition, size composition, and changes in abundance. Expected changes in absolute abundance, percent contribution to the population, and body size from early July to mid August are shown in Table 6 for various juvenile migration routes.

If only Hecate Strait tributaries contribute to the juvenile population in the Strait (Route 1) then all three species decline dramatically in abundance during July and are gone by mid August. Proportionately, the contribution by species doesn't change greately in July although pink decline and chum increase slightly, but by mid August all species have disappeared. Sizes remain small throughout.

If both central coast and Hecate Strait tributaries contribute to the population (Route 2) then abundance of all species still declines throughout July and August, however, the proportion of chum in the population increases. Pink and chum would still be present in small numbers in mid August and size of all species is predicted to be considerably larger.

If northern Georgia/Johnstone/Queen Charlotte Strait tributaries as well as central coast and Hecate Strait tributaries contribute to the population (Route 3) then sockeye and pink decline in abundance through July and August but chum do not decline until August. The proportion of sockeye in the population declines in July whereas the proportion of pinks remains the same or increases and the proportion of chum increases. The proportion of sockeye continues to decline in August whereas pink remain about the same and chum continue to increase. Mean size of all species is larger still, particularly in the mid August samples.

If all juveniles from the south inside waters migrate through Hecate Strait (Route 4) then sockeye and odd brood year pinks increase in abundance during July and decrease in August. Even brood year pink salmon decrease throughout July and August whereas chum remain constant during July then decline in August. Proportionately, the contribution of sockeye, odd brood year pinks, and chum remains the same or increase slightly, whereas even brood year pinks decrease. Sizes of sockeye and odd brood year pinks are larger whereas even brood year pinks and chum are about the same size as under Route 3. Predictions for route 5 are essentially the same as for route 4 (Table 6).

These differences in expected patterns of abundance and body size suggest that information collected during July and early August on abundance (catch-per-effort for example), species percent composition, and body length would permit the various migration route alternatives to be distinguished. Knowing the migratory routes of juveniles from different areas of the coast would permit preliminary estimates of absolute abundance based on model predictions. Further sampling programs could then be designed to confirm model estimates of abundance and food requirements. Sampling to evaluate migration routes was conducted during July and August of 1986 and 1987. As noted in the introduction, the results of this sampling will be reported elsewhere.

ACKNOWLEDGMENTS

Dr. Al Tyler, coordinator of the Hecate Strait project, provided encouragement and support throughout. I am indebted to many colleagues who shared with me their information and speculations about juvenile salmon behaviour during early sea life.

REFERENCES

Carl, L. M. and M. C. Healey. 1984. Differences in enzyme frequency and body morphology among three juvenile life history types of chinook salmon (Oncorhynchus tshawytscha) in the Nanaimo River, British Columbia. Can. J. Fish. Aquat. Sci. 41: 1070-1077.

Bailey, M. 1979. Enumeration of salmon in the Fraser River. Unpub. MS, Can. Dept. Fish. Oceans, Vancouver, B.C.: 121 p.

Barraclough, W. E. and A. Phillips. 1978. Distribution and abundance of juvenile salmon in the southern Strait of Georgia during the period April to July from 1966 to 1969. Can. Fish. Mar. Serv. Tech. Rep. 826: 47p.

Brett, J. R. and J. A. McConnell. 1950. Lakelse lake sockeye survival. J. Fish. Res. Board Can. 8: 103-110.

Fisher, J. P. and W. G. Pearcy. 1988. Growth of juvenile coho salmon (Oncorhynchus kisutch) in the ocean off Oregon and Washington, USA, in years of differing coastal upwelling. Can. J. Fish. Aquat. Sci. 45: 1036-1044.

Foerster, R. E. 1968. The sockeye salmon. Fish. Res. Board Can. Bull. 162: 422 p.

Groot, C. and K. Cooke. 1987. Are the migrations of juvenile and adult Fraser River sockeye salmon (Oncorhynchus nerka) in nearshore waters related? pp 53-60 In: H. D. Smith, L. Margolis, and C. C. Wood (ed.) Sockeye salmon (Oncorhynchus nerka) population biology and future management. Can. Spec. Pub. Fish. Aquat. Sci. 96.

Hartt, A. C. and M. B. Dell. 1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. Int. N. Pacific Fish. Comm. Bull. 46: 105 p.

Healey, M. C. 1967. Orientation of pink salmon (Oncorhynchus gorbuscha) during early marine migration from Bella Coola River system. J. Fish. Res. Board Can. 24: 2321-2338.

Healey, M. C. 1978. The distribution, abundance, and feeding habits of juvenile Pacific salmon in Georgia Strait, British Columbia. Fish. Mar. Serv. Tech. Rep. 788: 49p.

Healey, M. C. 1979. Detritus and juvenile salmon production in the Nanaimo estuary: I. Production and feeding rates of juvenile chum salmon (Oncorhynchus keta). J. Fish. Res. Board Can. 36: 488-496.

Healey, M. C. 1980. The ecology of juvenile salmon in Georgia Strait, B.C. pp 203-229 In: W. J. McNeill and D. C. Himsworth (eds). Salmonid Ecosystems of the North Pacific. Oregon State University Press, Corvallis, OR.

Healey, M. C. 1982. Juvenile Pacific salmon in estuaries: the life support system. pp 315-341 In: V. S. Kennedy (ed.) Estuarine Comparisons, Academic Press, New York, NY.

Healey, M. C. 1983. Coastwide distribution and ocean migration patterns of stream- and ocean-type chinook (Oncorhynchus tshawytscha). Can. Field-Nat. 97: 427-433.

Healey, M. C. 1986. Optimum size and age at maturity in Pacific salmon and effects of size selective fisheries. pp 39-52 In: D. J. Meerburg (ed.), Salmonid Age at Maturity. Can. Spec. Pub. Fish. Aquat. Sci. 89.

Holtby, L. B. and G. F. Hartman. 1982. The population dynamics of coho salmon (Oncorhynchus kisutch) in a west coast rain forest stream subjected to logging. pp 308-347 In: G. Hartman (ed.) Proceedings of the Carnation Creek workshop, a 10 year review. Available from Dept. of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., V9R 5K6.

Hunter, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16: 835-886.

Hyatt, K. D., D. Rutherford, T. Gjernes, P. Rankin, and T. Cone. 1984. Lake enrichment program: juvenile sockeye unit survey guidelines. Can. MS Rep. Fish. Aquat. Sci. 1796: 84 p.

Johnson, W. E. and C. Groot. 1963. Observations on the migration of young sockeye salmon (Oncorhynchus nerka) through a large, complex lake system. J. Fish. Res. Board Can. 20: 919-938.

LeBrasseur R. J. and W. Barner. 1964. Midwater trawl salmon catches in northern Hecate Strait, November, 1963. Fish. Res. Board Can. MS Rep. 176: 7p + tables.

Lister, D. B. and C. E. Walker. 1966. The effect of flow control on freshwater survival of chum, coho and chinook salmon in the Big Qualicum River. Can. Fish. Cult. 37: 3-25.

Manzer, J. I. 1956. Distribution and movement of young Pacific salmon during early ocean residence. Fish. Res. Board Can. Progress Rep. Pacific 106: 24-28.

Manzer, J. I. and I. Miki. 1986. Fecundity and egg retention of some sockeye salmon (Oncorhynchus nerka) stocks in British Columbia. Can. J. Fish. Aquat. Sci. 43: 1643-1655.

Miller, D. R., J. G. Williams, and C. W. Sims. 1982. Distribution, abundance, and growth of juvenile salmonids off the coast of Gregon and Washington, summer 1980. Fish. Res. 2: 1-17.

NOAA. 1984. Cruise Report of the Drum Seiner F/V Bering Sea. Coastwide NWAFC/OSU cooperative study ecology of juvenile salmon in coastal and inside waters of southeast Alaska, 28 June - 26 July 1984. Mimeo Report available from Northwest and Alaska Fisheries Center, Auke Bay Laboratory, Auke Bay, AK.

Parker, R. R. 1965. Estimation of sea mortality rates for the 1961 brood-year pink salmon of the Bella Coola area, British Columbia. J. Fish. Res. Board Can. 22: 1523-1554.

Parker, R. R. 1966. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25: 757-794.

Pearcy, W. G. 1984. Where do all the coho go? The biology of juvenile coho salmon off the coasts of Washington and Oregon. pp 50-60 In: W. G. Pearcy (ed.) The influence of ocean conditions on the production of salmonids in the North Pacific. Oregon State University, Sea Grant College Program, Corvallis, OR.

Phillips, A. and W. E. Barraclough. 1978. Early marine growth of juvenile Pacific salmon in the Strait of Georgia and Saanich Inlet, British Columbia. Can. Fish. Mar. Serv. Tech. Rep. 830: 19p.

Tyler, A. V. 1986. Hecate Strait project: Results of the first two years of multispecies fisheries research. Can. Tech. Rep. Fish. Aquat. Sci. 1470: 1-50.

Wakefield, W. W., J. P. Fisher, and W. G. Pearcy. 1981. Studies of juvenile salmonids off the Oregon and Washington coast, 1981. Oregon State University, School of Oceanography, Corvallis OR. Cruise Report Reference 81-13: 51p.

Table 1. Annual escapement by species (1973-1982 averages) to each coastal compartment of the migration model, estimated juvenile production per compartment, and assumptions underlying juvenile production estimate. Fishery statistical areas included within each coastal compartment shown in brackets after compartment name in escapement section.

Compartment	Sockeye	Pink Odd	Pink Even	Chum	Coho	Chinook
Escapement (thousands)						
Dixon Ent. (1,3,4)	1116	1298	1983	126	115	33
Hecate Str. (2E,5,6)	56	456	1980	351	97	8
Central Coast (7 - 11)	666	323	1866	408	59	23
Johnstone/N Geo. Str. (12-16)	72	665	1136	595	128	23
W. Vancouver Is. (20-27)	325	3	294	464	90	21
S. Georgia Str. (17-19,28,29)	1613	1686	0	756	154	82
Juvenile Production (millions)	(a)	(b)	(c)	(d)	(e)	(f)
Dixon Ent.	25.78	39.20	44.91	5.71	5.46	4.12
Hecate Str.	1.29	13.77	44.84	15.90	4.61	1.00
Central Coast	15.38	9.75	42.26	18.48	2.80	2.88
Jhnstn/N.Geo.Str.	1.66	20.08	25.73	26.95	6.08	2.88
W. Vancouver Is.	7.51	0.091	6.66	21.02	4.27	2.62
S. Georgia Str.	37.26	50.92	0.00	34.25	7.31	10.25

(a) Juveniles = escapement X 3400(eggs/fem.) X 0.5(proportion female) X .014(freshwater and coastal survival up to time of northward migration)
(b) Juveniles = escapement X 2000 X 0.5 X 0.03
(c) Juveniles = escapement X 1500 X 0.5 X 0.03
(d) Juveniles = escapement X 3000 X 0.5 X 0.03
(e) Juveniles = escapement X 3500 X 0.014. Note: assumes escapement estimate underestimates true escapement by 1/2.
(f) Juveniles = escapement X 5000 X .025. Note: assumes escapement estimate underestimates true escapement by 1/2.

Table 2. Some output values from the model for extreme assumptions about juvenile migratory behaviour.

Output	Species					
	Sockeye	Pink (odd)	Pink (even)	Chum	Coho	Chinook
Migration Assumption: - Only salmon from rivers tributary to Hecate Strait migrate through the strait (Route 1, see Table 4).						
Appear (wk)	20	19	19	20	19	27
Disappear (wk)	28	31	31	32	33	41
Peak No. (wk)	24	25	25	26	25	33
No. at Peak (millions)	0.65	6.48	21.1	7.48	4.22	0.91
Max. Length (mm)	104.2	84.0	84.0	85.5	149.0	122.0
Food Eaten (tons)	16.5	237.7	774.1	221.9	650.2	79.5
Migration Assumption: - All salmon from rivers tributary to Hecate Strait and south to southern Strait of Georgia migrate north through Hecate Strait (Route 5, see Table 4).						
Appear (wk)	20	19	19	20	19	27
Disappear (wk)	36	39	39	41	52*	52*
Peak No. (wk)	31	31	26	32	25	46
No. at Peak (millions)	28.9	18.2	36.5	19.8	4.22	1.72
Max. Length (mm)	146.2	154.0	154.0	143.2	321.4	203.7
Food Eaten (tons)	2319.8	3317.0	3267.4	2501.9	4037.2	647.0

* Simulations terminated at week 52.

Table 3. Percent composition of sockeye, pink, and chum salmon in Hecate Strait during even and odd years in early July (week 27), late July (week 30) and mid August (week 33) under different assumptions about migratory route. See Table 4 for a description of the routes.

		Even Years			Odd Years		
Week	Route	Sockeye	Pink	Chum	Sockeye	Pink	Chum
27	1	1	38	61	+	66	33
30		0	26	74	0	54	46
33		0	0	0	0	0	0
27	2	31	26	44	18	57	25
30		7	21	72	4	53	43
33		0	10	90	0	33	67
27	3	29	29	42	17	57	26
30		7	34	58	5	53	41
33		1	31	68	1	41	58
27	4	33	30	38	21	54	24
30		41	30	29	40	32	28
33		30	36	33	40	15	44
27	5	33	29	38	22	54	24
30		44	27	29	42	30	28
33		31	30	39	37	16	46

Table 4. Summary of food resource demands (metric tons of food organisms) by juvenile salmon in Hecate Strait under different assumptions about migratory routes.

Species	Migratory Route	Month May	June	July	Aug.	Sept.	Oct.
Sockeye	1	1	15	1	0	0	0
	2	3	301	177	2	0	0
	3	3	307	220	13	0	0
	4	3	314	822	878	5	0
	5	3	316	943	1052	6	0
	6	3	273	282	1155	121	0
Pink (odd)	1	17	164	55	1	0	0
	5	18	314	1006	1774	204	0
	6	18	293	500	1166	582	30
Pink (even)	1	55	535	180	3	0	0
	5/6	62	1034	1377	755	39	0
Chum	1	6	130	81	4	0	0
	2	6	220	355	134	1	0
	3	6	230	522	442	25	0
	4	6	230	566	942	259	11
	5	6	230	625	1282	347	12
	6	6	230	581	956	567	141
Coho	1	22	299	297	32	0	0
	5	22	299	299	300	476	566
Chinook	1	0	0	7	43	28	1
	5	0	0	7	43	28	60

Migratory Routes:
1. Only juveniles from tributaries of Hecate Strait.
2. Juveniles from Hecate Strait and Central Coast.
3. Juveniles from Hecate Strait, Central Coast, and Northern Georgia Strait.
4. Juveniles from Hecate Strait, Central Coast, Northern and Southern Georgia Strait.
5. Juveniles from all compartments south of Hecate Strait. Juveniles from Southern Georgia Strait migrate north via Johnstone and Queen Charlotte Straits.
6. Juveniles from all compartments south of Hecate Strait. Juveniles from Southern Georgia Strait migrate north via Juan de Fuca Strait and the West Coast of Vancouver Island.

Table 5. Some output of model when growth rates (mm/wk) were varied for sockeye, pink (odd), and chum salmon.

Output \ Growth ->	Sockeye 4.2	Sockeye 7.0	Pink 7.0	Pink 8.4	Chum 5.25	Chum 7.0
(Juveniles from Hecate Trib's Only: Route 1)						
Peak # (millions)	0.6	0.6	6.5	6.5	7.5	7.5
Max. Length (mm)	104	107	84	87	86	89
Peak Biomass (t)	7.4	7.7	29	31	40	43
Food Needs (t)	16	29	238	303	222	318
(All Juveniles from South: Route 5)						
Peak # (millions)	29	24	18	15	20	22
Max. Length (mm)	146	170	154	162	143	159
Peak Biomass (t)	925	1227	596	608	478	766
Food Needs (t)	2320	4030	3317	3692	2502	4368

Table 6. Expected changes in absolute abundance, in percent contribution to the population, and in expected absolute sizes of sockeye, pink, and chum salmon in Hecate Strait from early July to late August. D and U indicate downward or upward changes in absolute abundance of > 40% or an absolute change in percent contribution of > 15%. d and u indicate downward or upward changes in absolute abundance of 10-40% or an absolute change in percent contribution of 5-15%. "=" indicates a change in absolute abundance of < 10% or an absolute change in percent contribution of < 5%.

		Abundance		Percent Odd Years		Percent Even Years		Length (mm)		
		E-L	L-July	E-L	L-July	E-L	L-July	E	L	M
Rte	Spec	July	M-Aug	July	M-Aug	July	M-Aug	July	July	Aug
1	Sox	D	=	=	=	=	=	103	-	-
	Pink (o)	D	D	d	D	-	-	79	82	-
	Pink (e)	D	D	-	-	d	D	79	82	-
	Chum	D	D	u	D	u	D	81	82	-
2	Sox	D	D	D	d	d	d	117	120	-
	Pink (o)	D	D	=	d	-	-	90	101	110
	Pink (e)	D	D	-	-	=	D	91	101	110
	Chum	d	D	U	U	U	U	90	100	107
3	Sox	D	D	D	d	d	d	117	127	137
	Pink (o)	d	D	u	=	-	-	98	120	131
	Pink (e)	D	D	-	-	=	d	95	112	128
	Chum	=	D	U	u	U	U	92	107	118
4	Sox	U	D	u	d	U	=	121	137	143
	Pink (o)	U	d	=	u	-	-	102	129	141
	Pink (e)	D	D	-	-	D	D	95	112	128
	Chum	=	d	d	=	=	U	92	110	126
5	Sox	U	D	u	d	U	=	122	137	143
	Pink (o)	U	d	=	=	-	-	102	129	141
	Pink (e)	D	D	-	-	D	D	95	114	132
	Chum	U	=	d	u	=	U	92	112	127

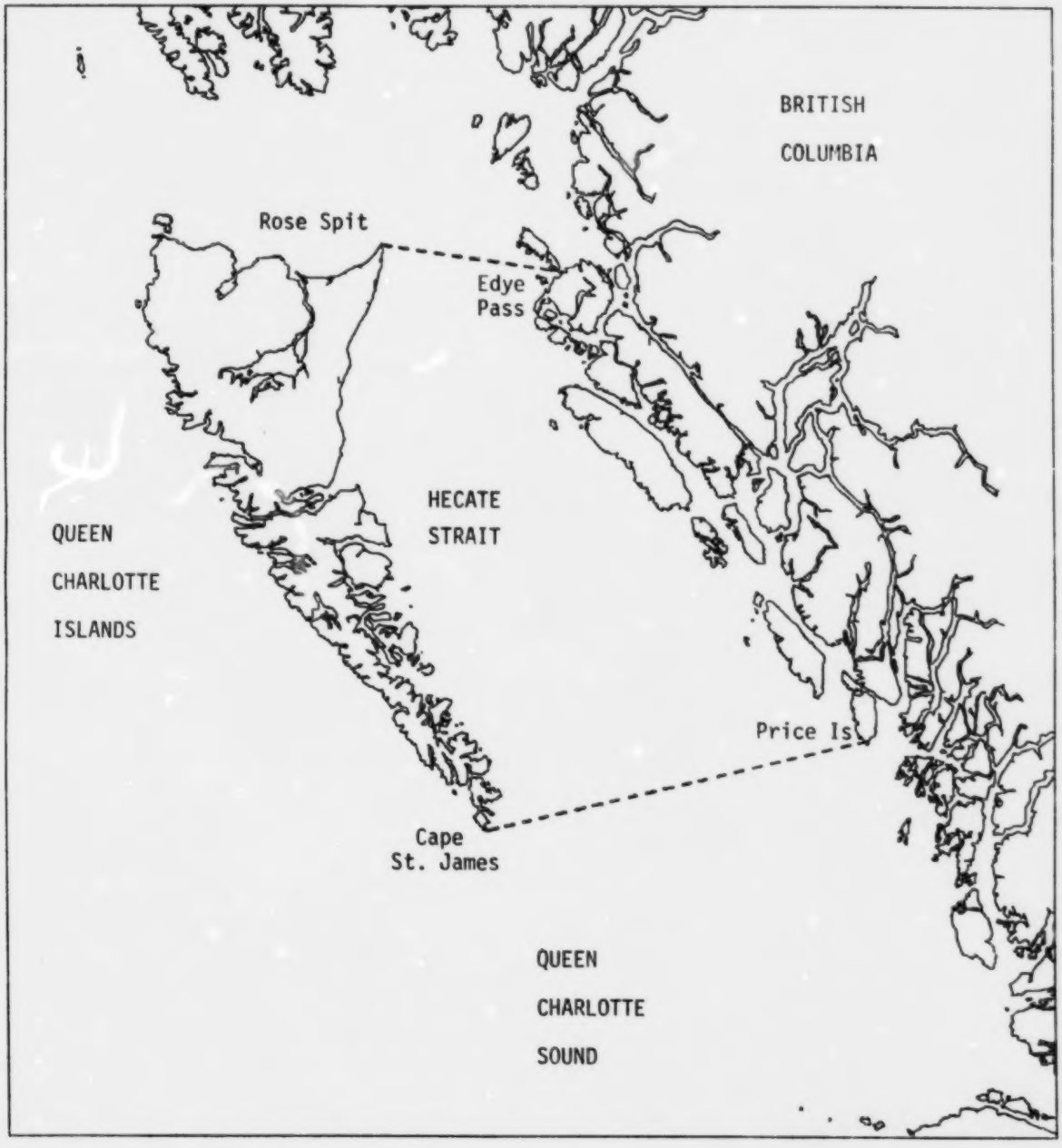

Fig. 1. Map of Hecate Strait, British Columbia, showing principal landmarks referred to in the text.

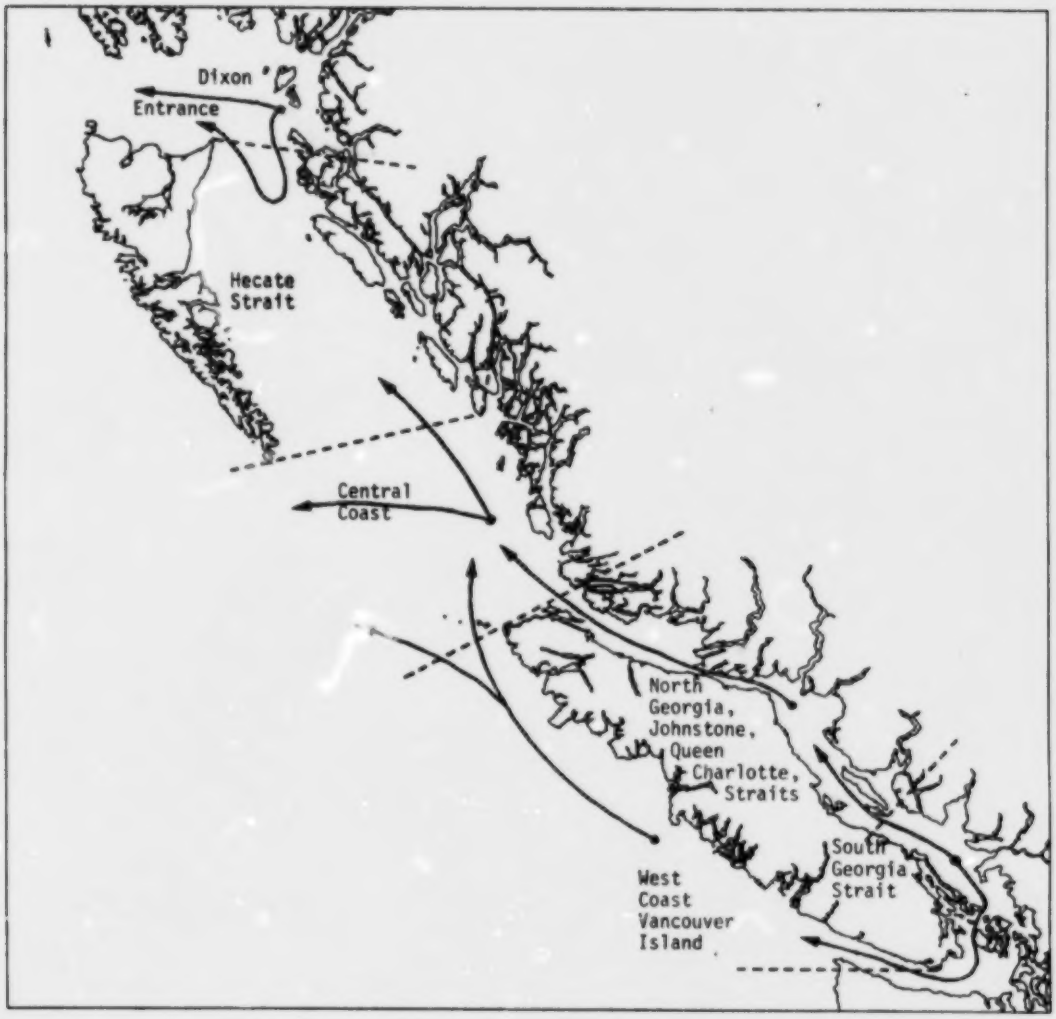

Fig. 2. Map of the British Columbia Coast showing coastal compartments used in the juvenile salmon migration model. Possible migration routes from each compartment to Hecate Strait or to bypass Hecate Strait are shown by arrows.

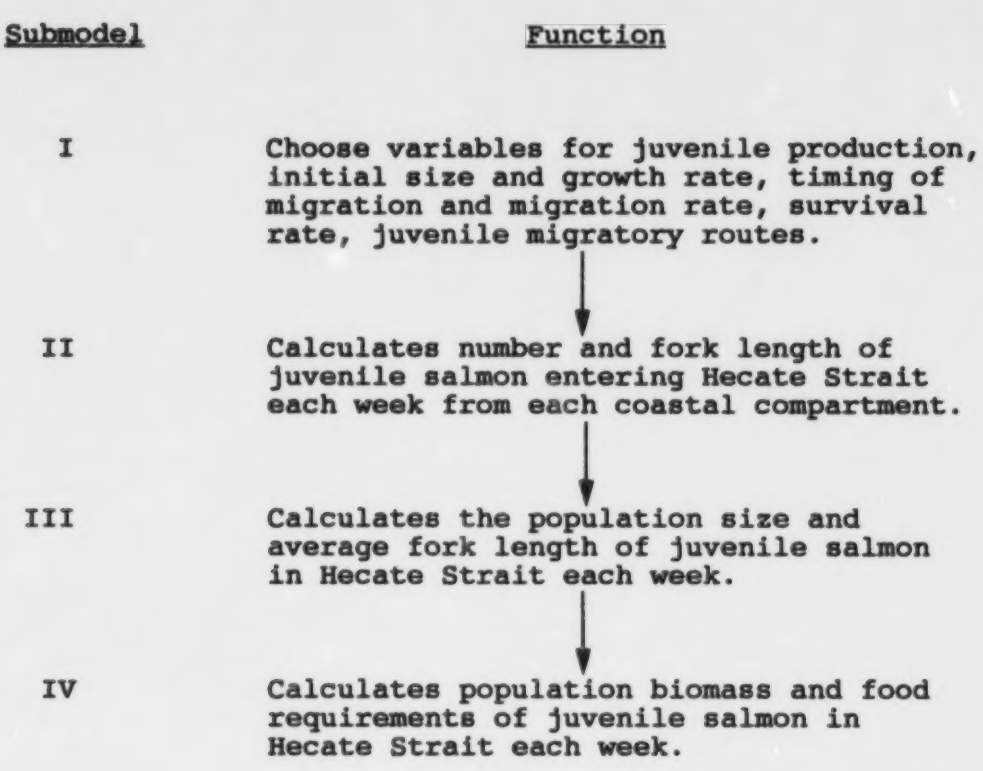
Submodel
Function
I
Choose variables for juvenile production, initial size and growth rate, timing of migration and migration rate, survival rate, juvenile migratory routes.
II
Calculates number and fork length of juvenile salmon entering Hecate Strait each week from each coastal compartment.
III
Calculates the population size and average fork length of juvenile salmon in Hecate Strait each week.
IV
Calculates population biomass and food requirements of juvenile salmon in Hecate Strait each week.

Fig. 3. Summary flow diagram for the juvenile salmon migration model.

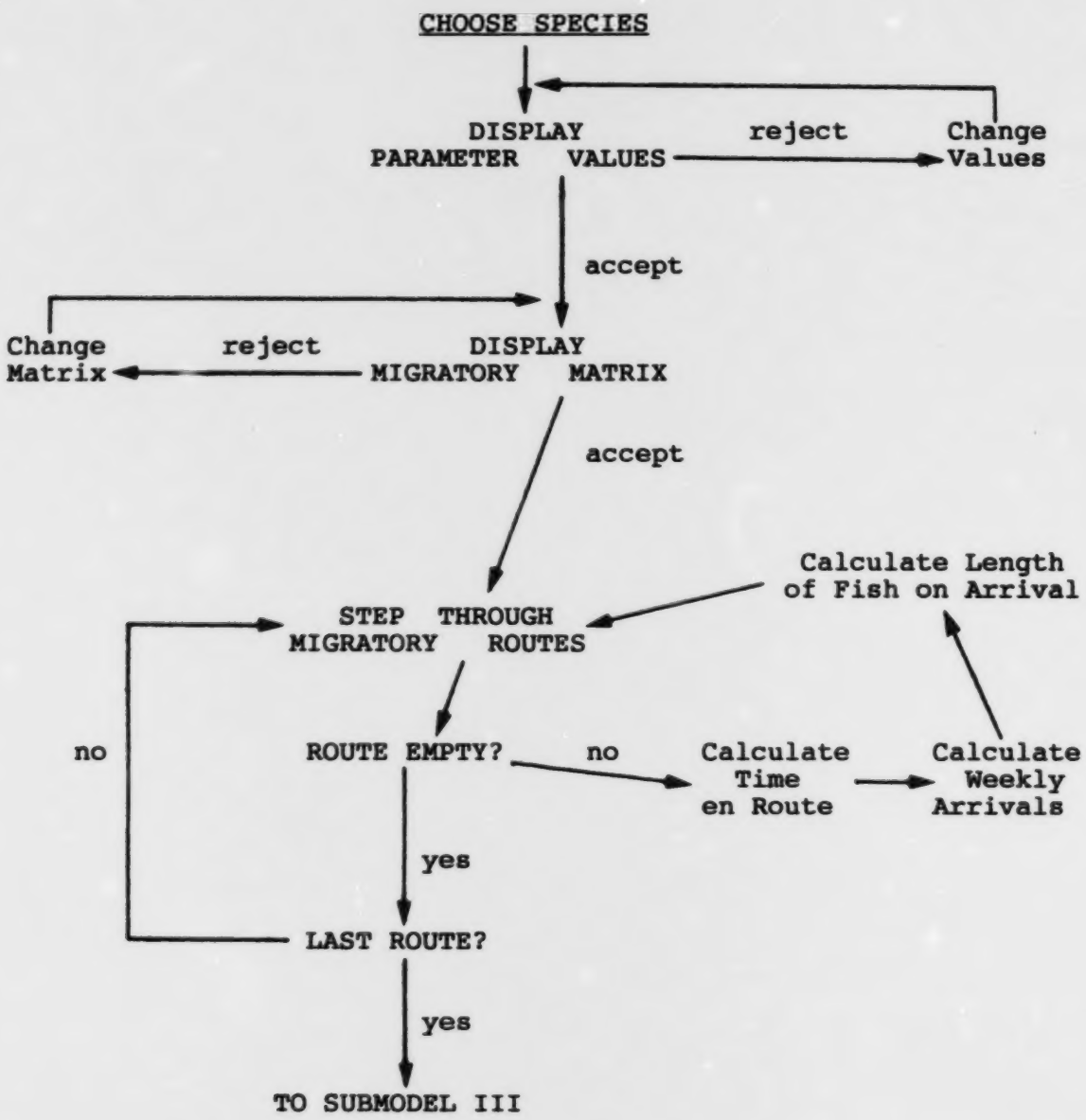

Fig. 4. Details of submodels I and II of the juvenile salmon migration model.

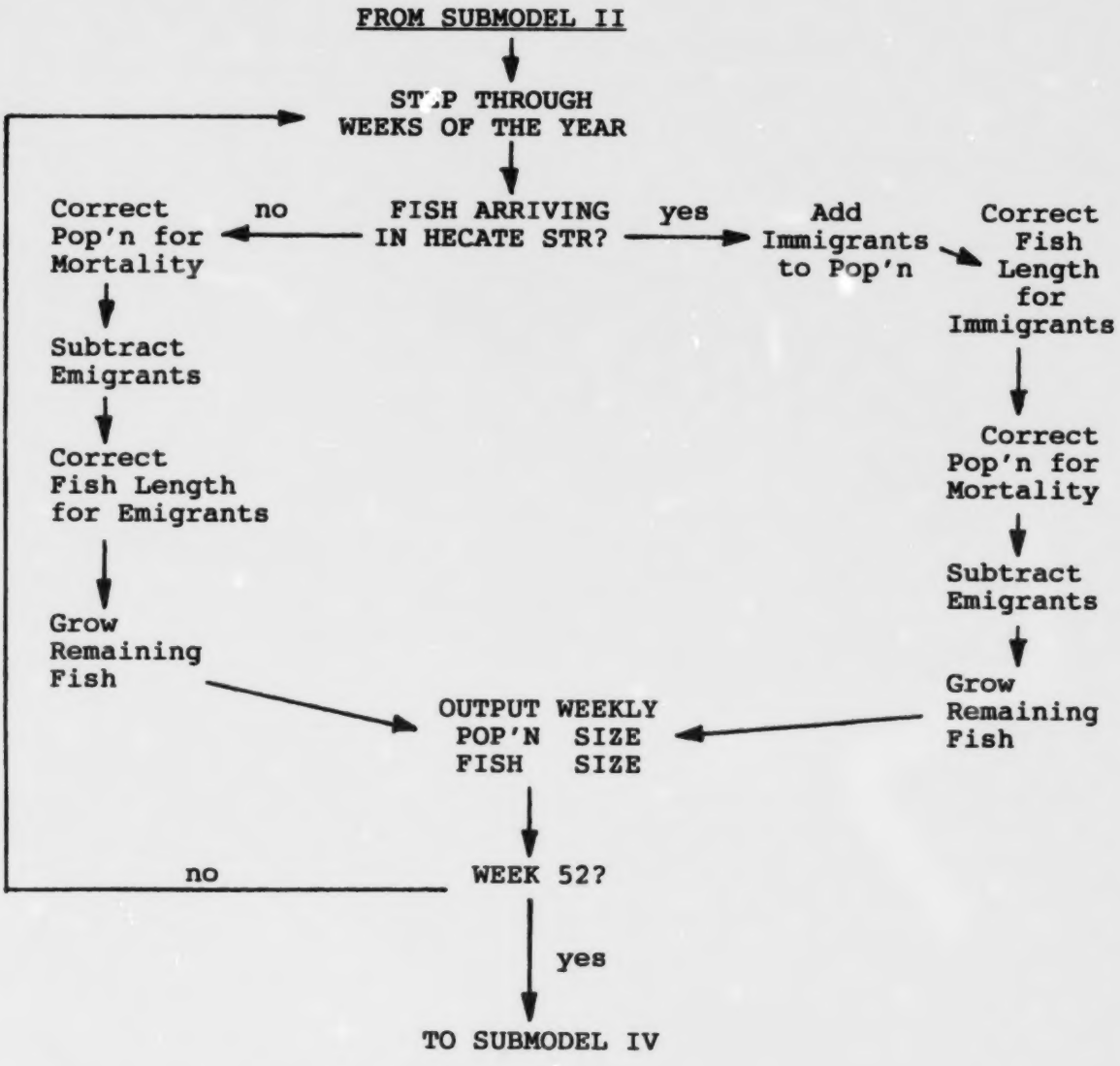

Fig. 5. Details of submodel III of the juvenile salmon migration model.

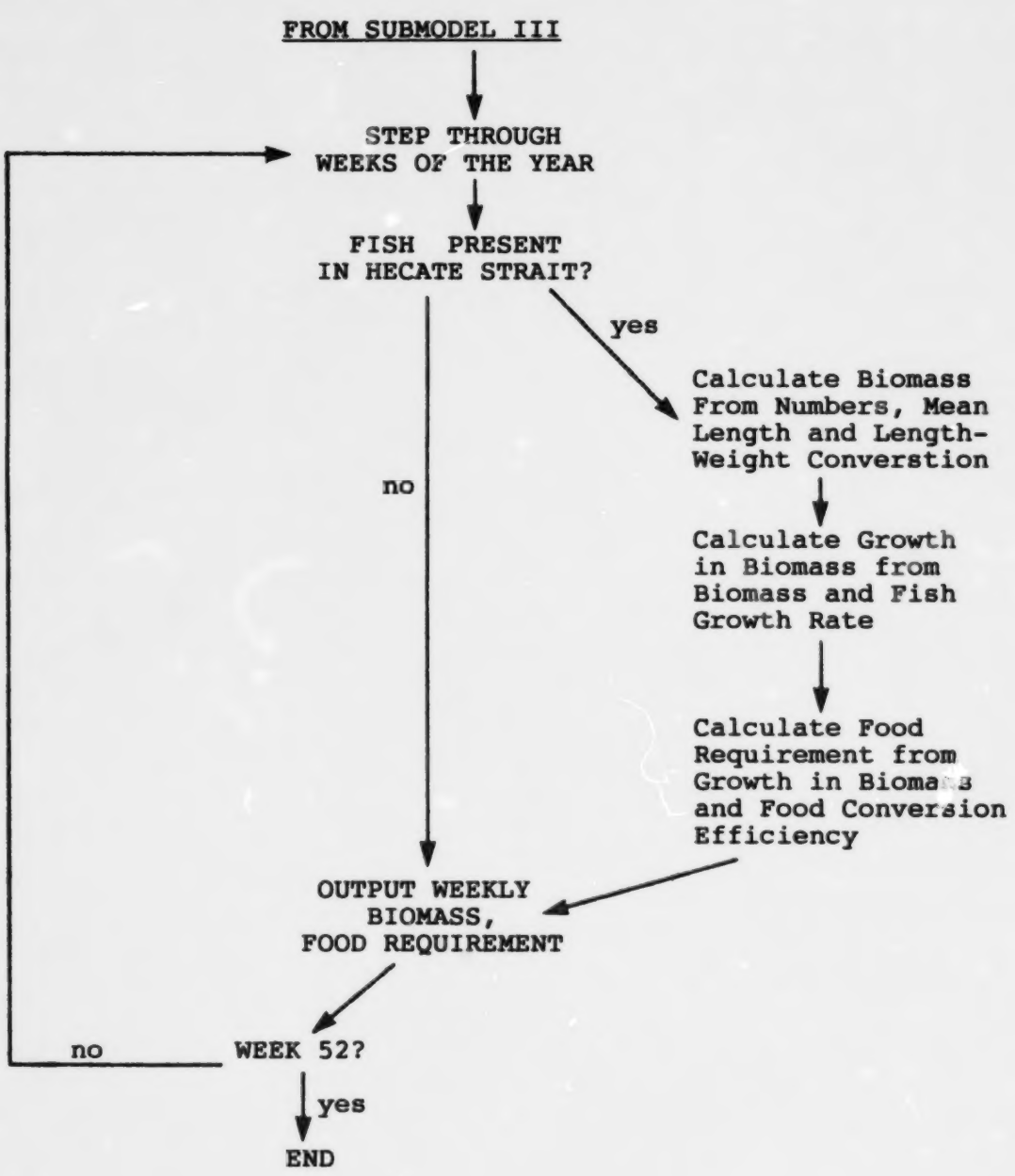
FROM SUBMODEL III
STEP THROUGH WEEKS OF THE YEAR
FISH PRESENT IN HECATE STRAIT?
yes
no
Calculate Biomass From Numbers, Mean Length and Length-Weight Converstion
Calculate Growth in Biomass from Biomass and Fish Growth Rate
Calculate Food Requirement from Growth in Biomass and Food Conversion Efficiency
OUTPUT WEEKLY BIOMASS, FOOD REQUIREMENT
WEEK 52?
no
yes
END

Fig. 6. Details of submodel IV of the juvenile salmon migration model.

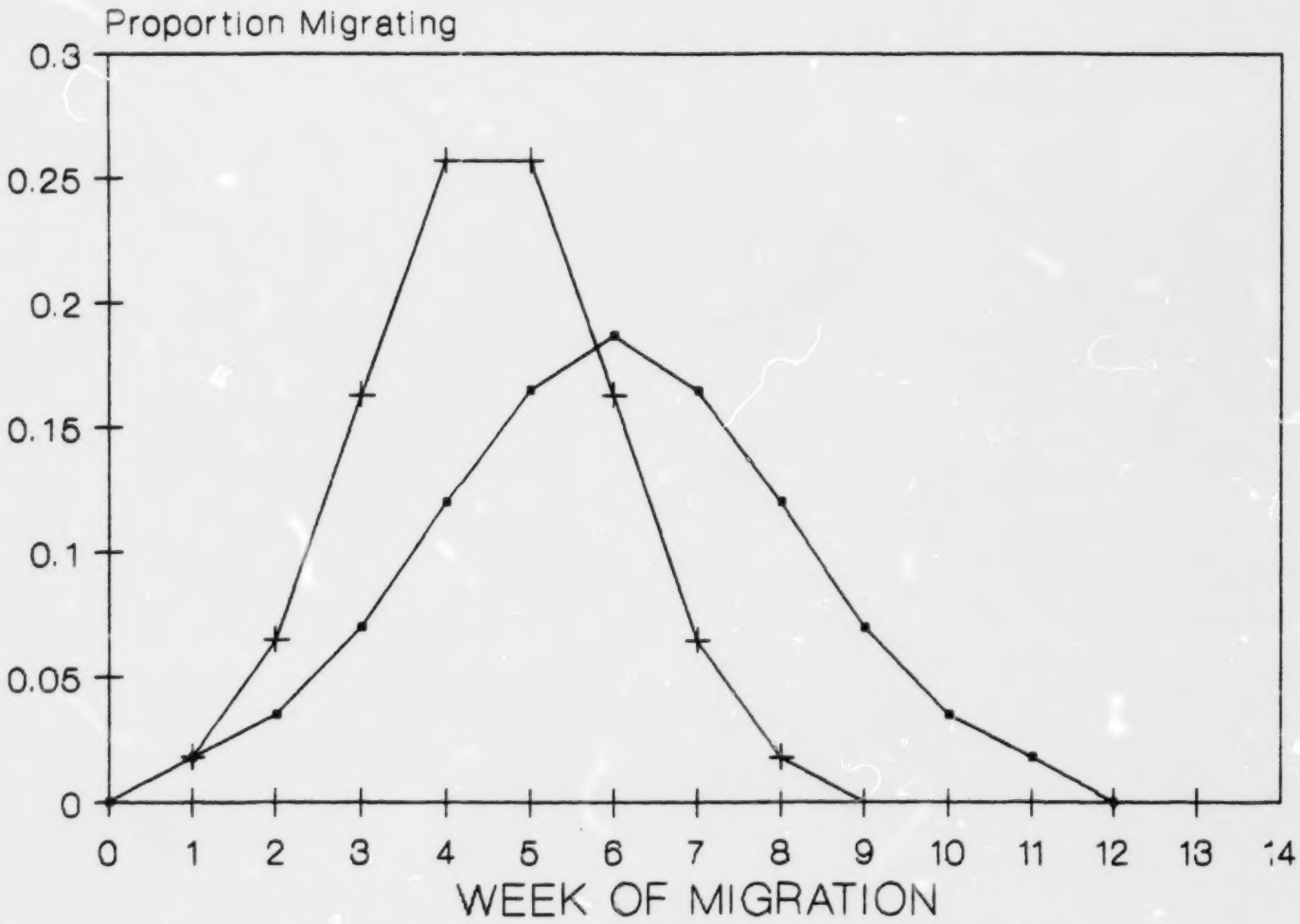

Fig. 7. Probability curves for the initiation of migration by the different salmon species. Curves show the proportion of the juvenile stock initiating migration during each week of the migration. (▪) Curve for pink and chum. (+) Curve for sockeye, coho, and chinook.

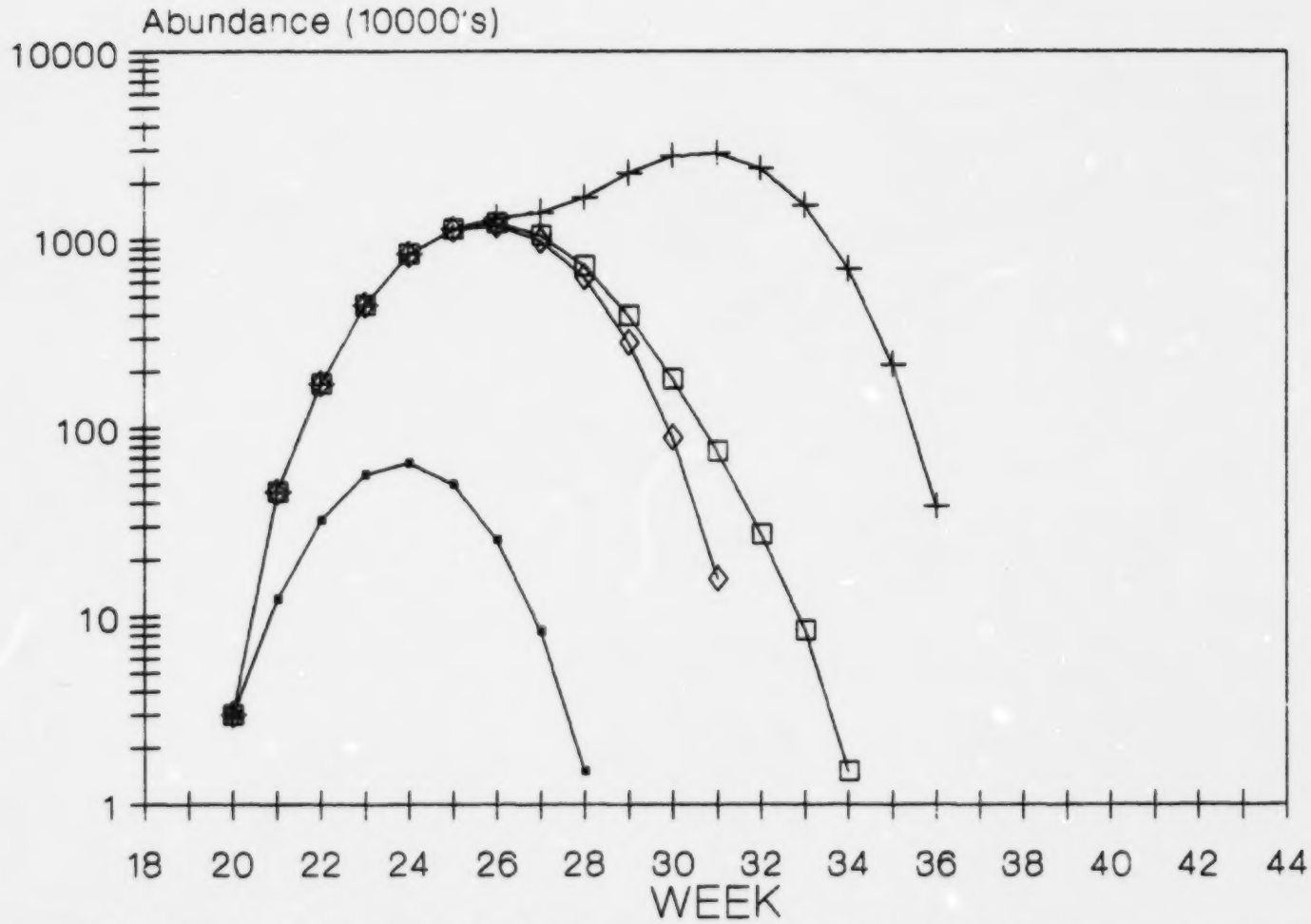

Fig. 8. Abundance curves for sockeye salmon in Hecate Strait under different migration route assumptions. (■) Route 1; (◊) Route 2; (□) Route 3; (+) Route 5. See Table 4 for description of routes.

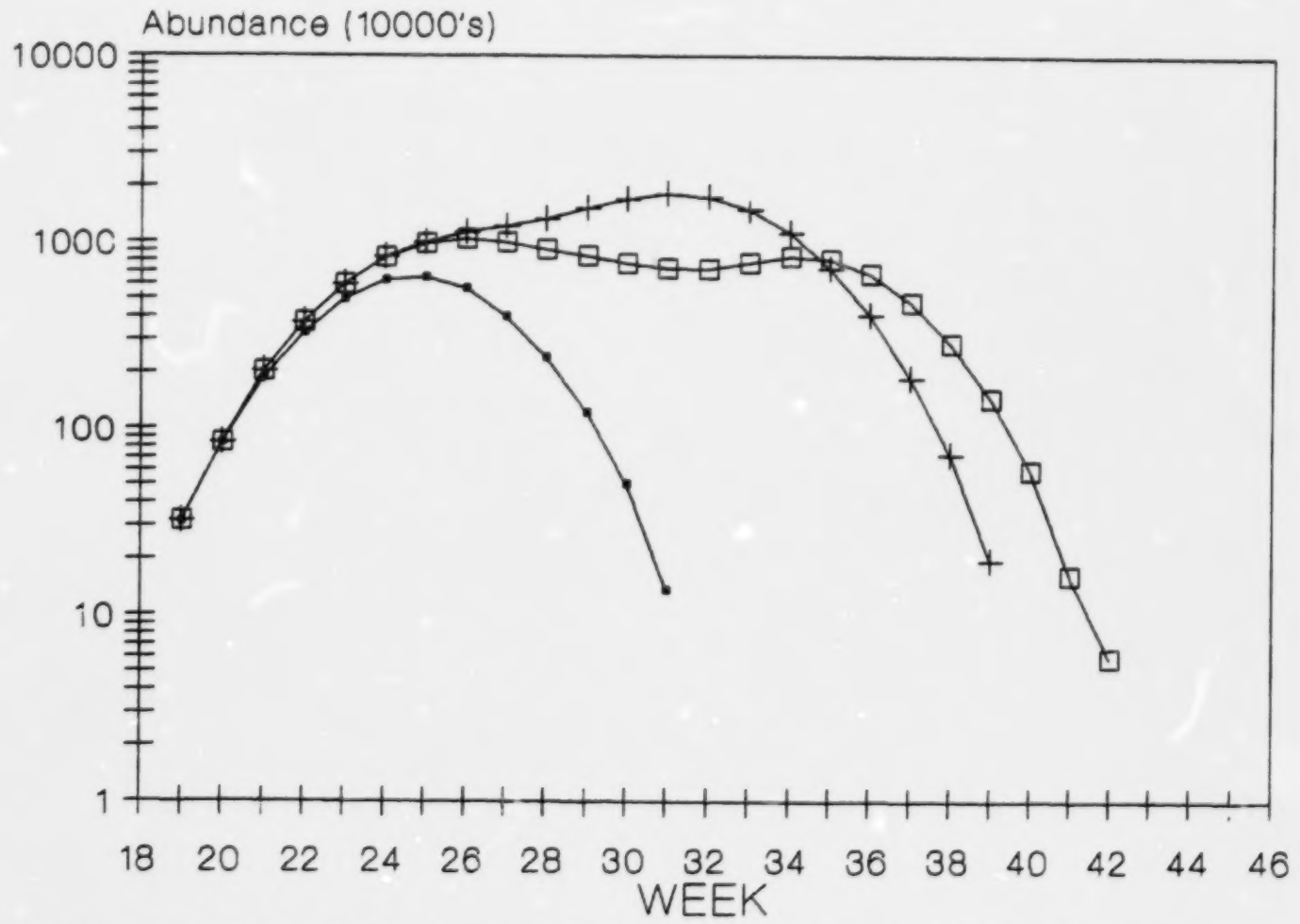

Fig. 9. Abundance curves for odd brood year pink salmon juveniles in Hecate Strait under different migration route assumptions. (■) Route 1; (+) Route 5; (□) Route 6. See Table 4 for description of routes.

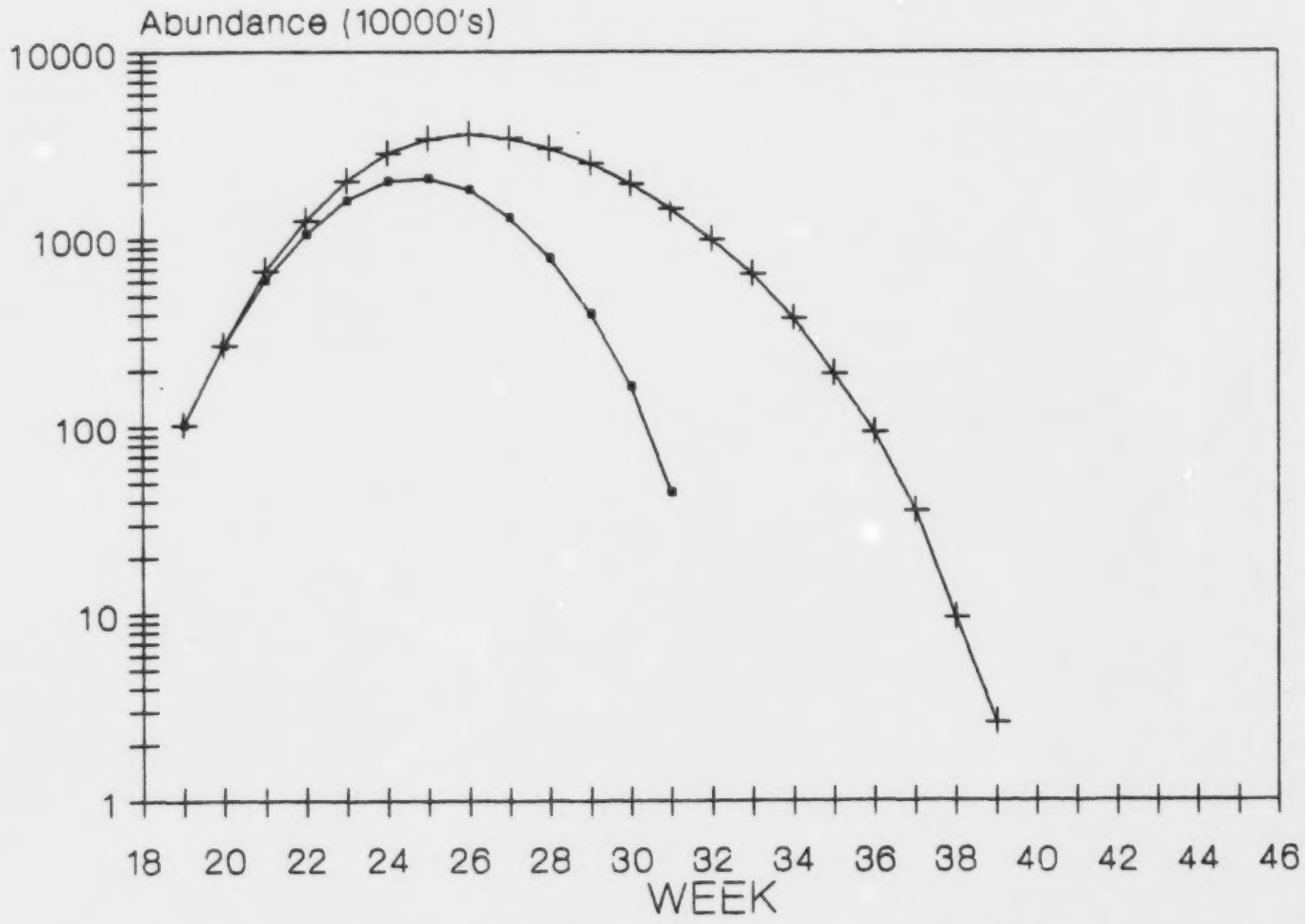

Fig. 10. Abundance curves for even brood year pink salmon juveniles in Hecate Strait under different migration route assumptions. (■) Route 1; (+) Route 5 or 6. See Table 4 for description of routes.

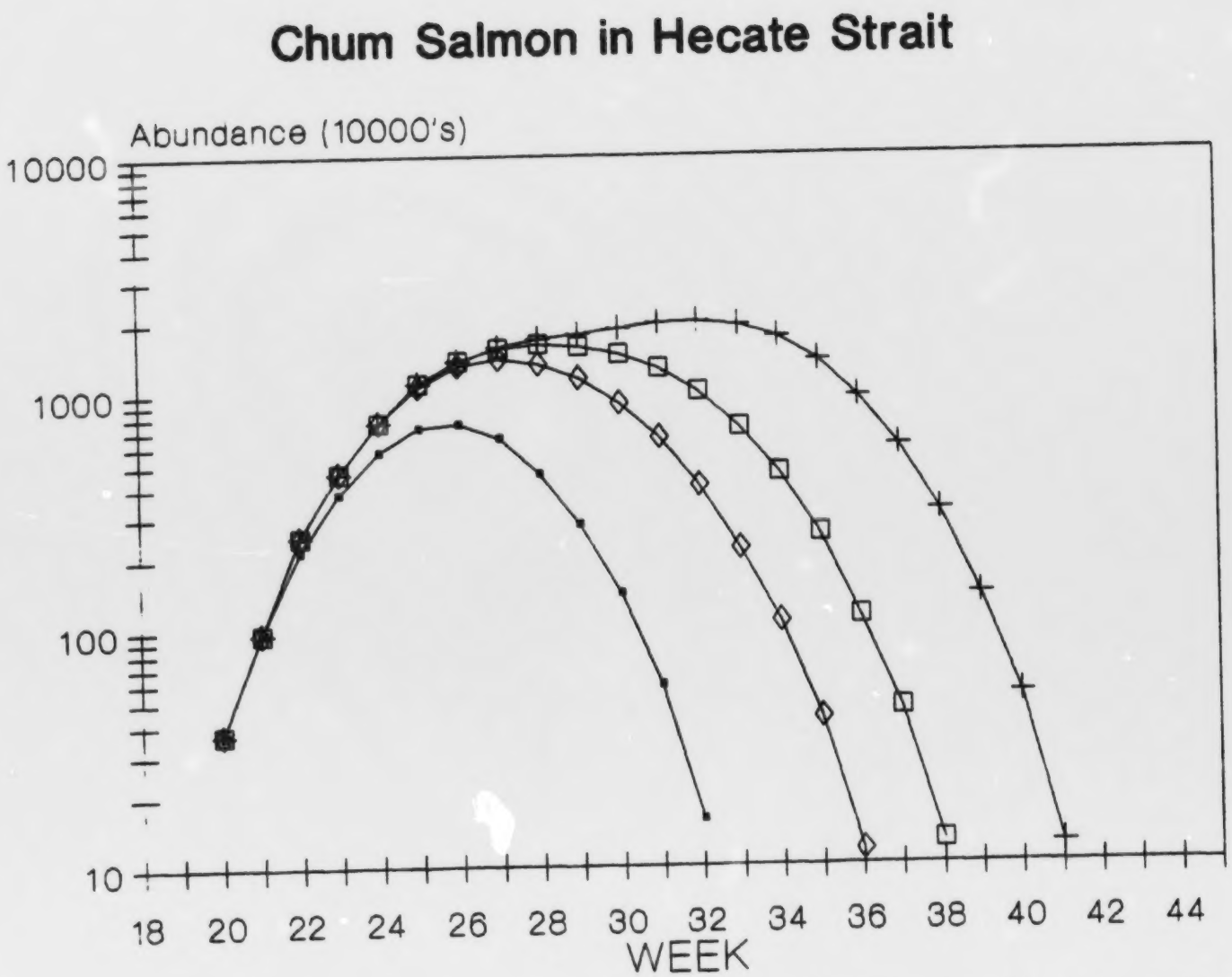

Fig. 11. Abundance curves for chum salmon in Hecate Strait under different migration route assumptions. (■) Route 1; (◊) Route 2; (□) Route 3; (+) Route 5. See Table 4 for description of routes.

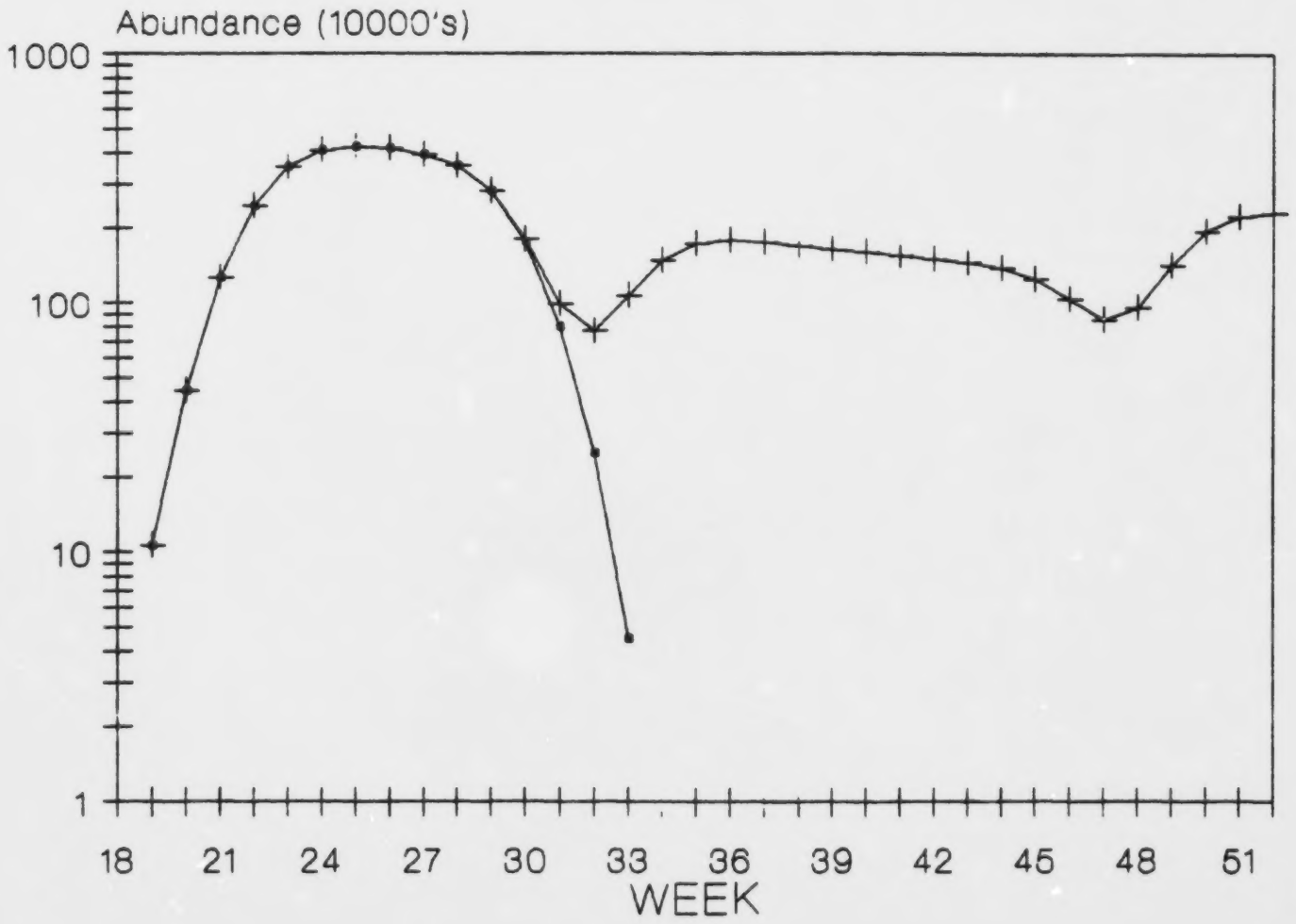

Fig. 12. Abundance curves for coho salmon in Hecate Strait under different migration route assumptions. (■) Route 1; (+) Route 5. See Table 4 for description of routes.

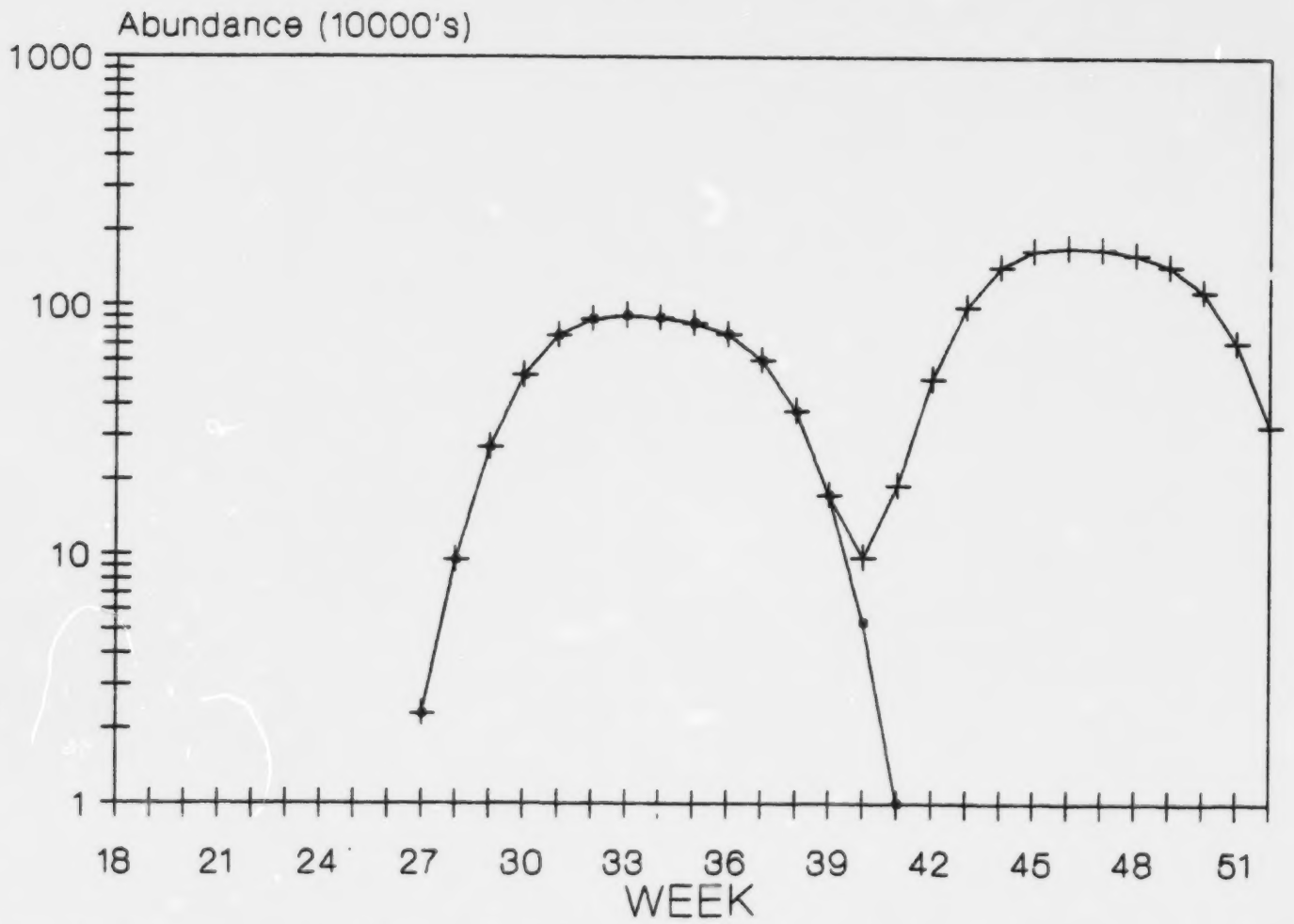

Fig. 13. Abundance curves for chinook salmon in Hecate Strait under different migration route assumptions. (■) Route 1; (+) Route 5. See Table 4 for description of routes.

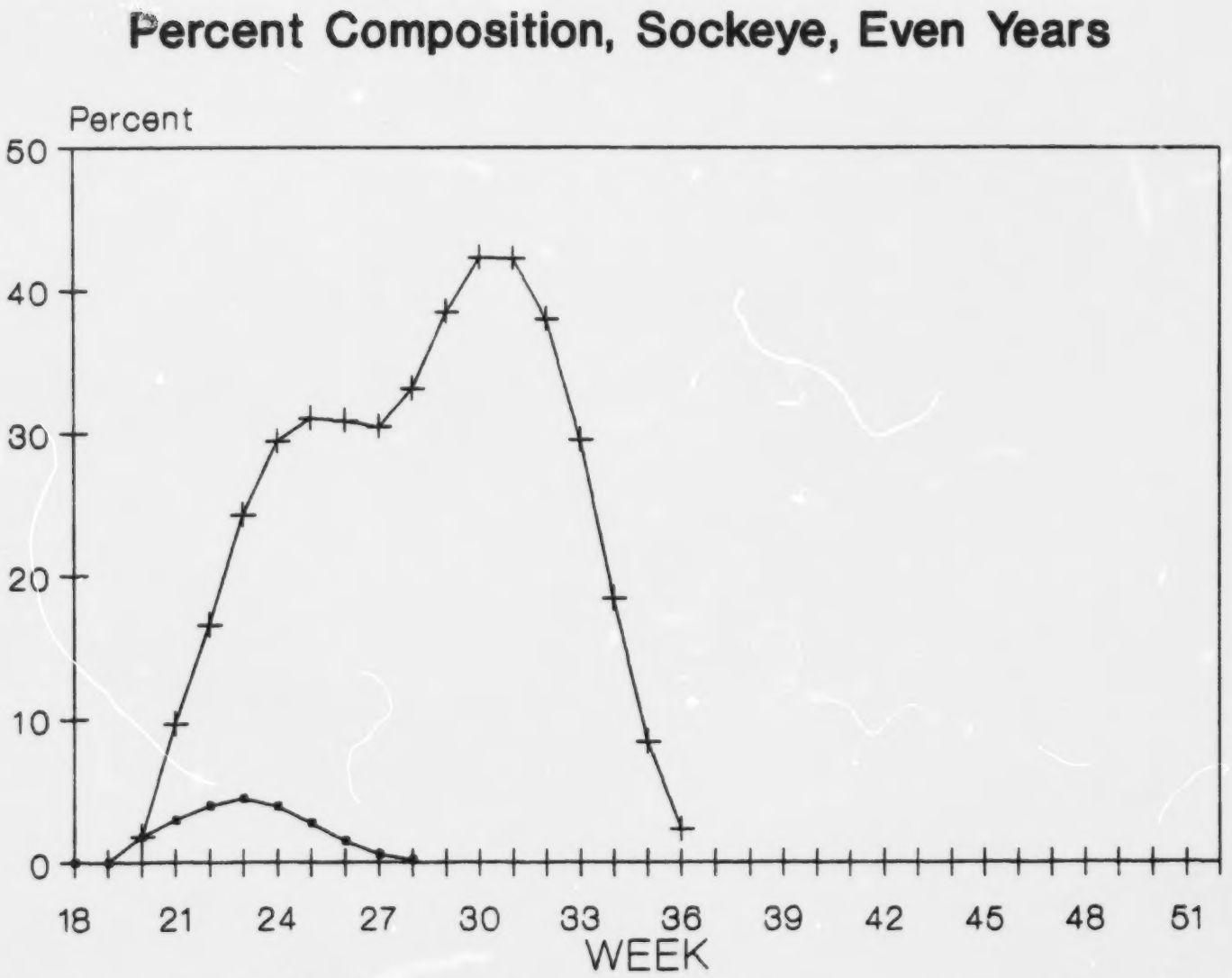

Fig. 14. Percent contribution of sockeye salmon in even years (when associated with odd brood year pink salmon) to the Hecate Strait juvenile salmon population each week if juveniles follow route 1 (▪) or route 5 (+).

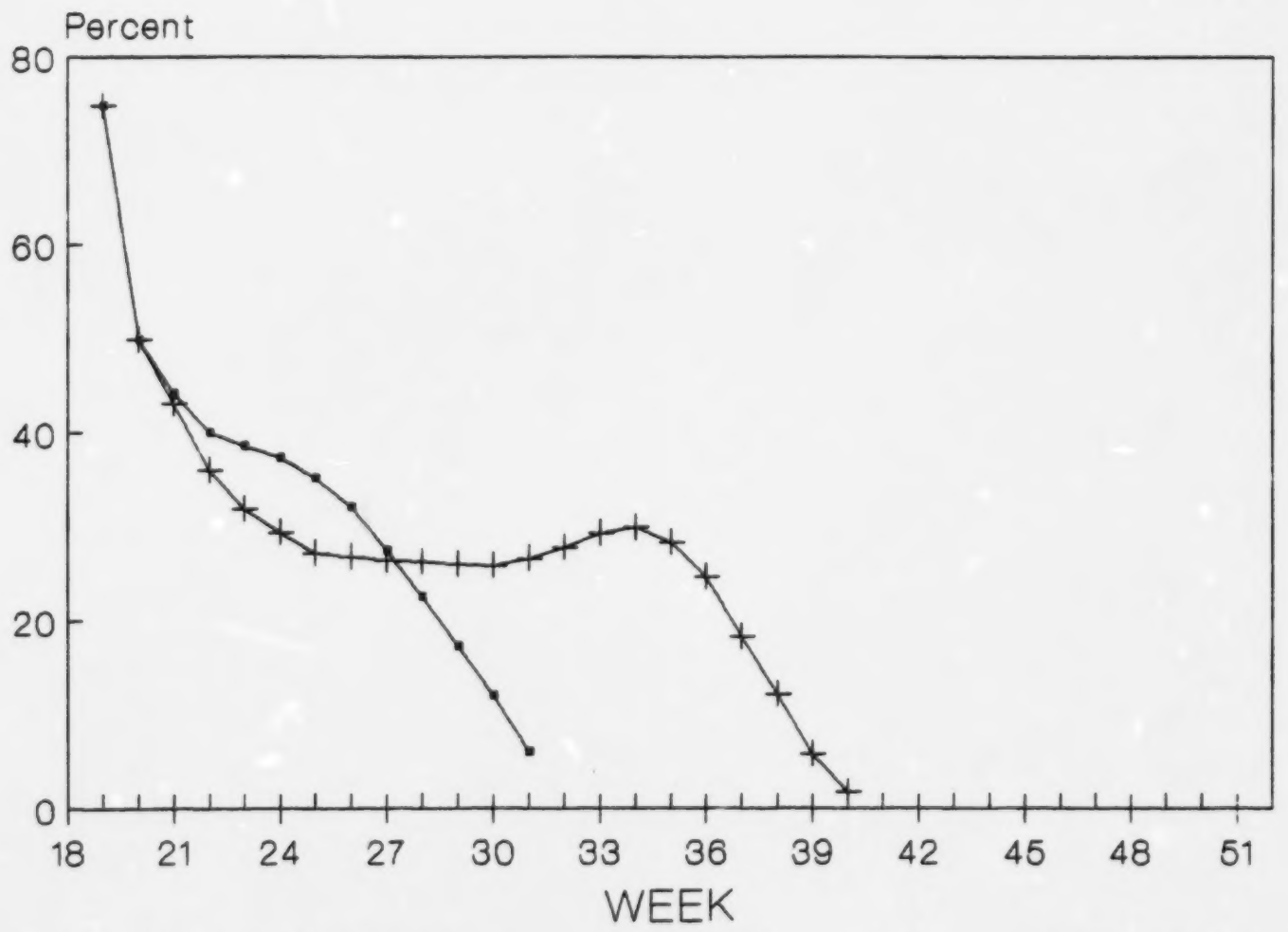

Fig. 15. Percent contribution of odd brood year pink salmon (even calendar year for juveniles) to the Hecate Strait juvenile salmon population each week if juveniles follow route 1 (■) or route 5 (+).

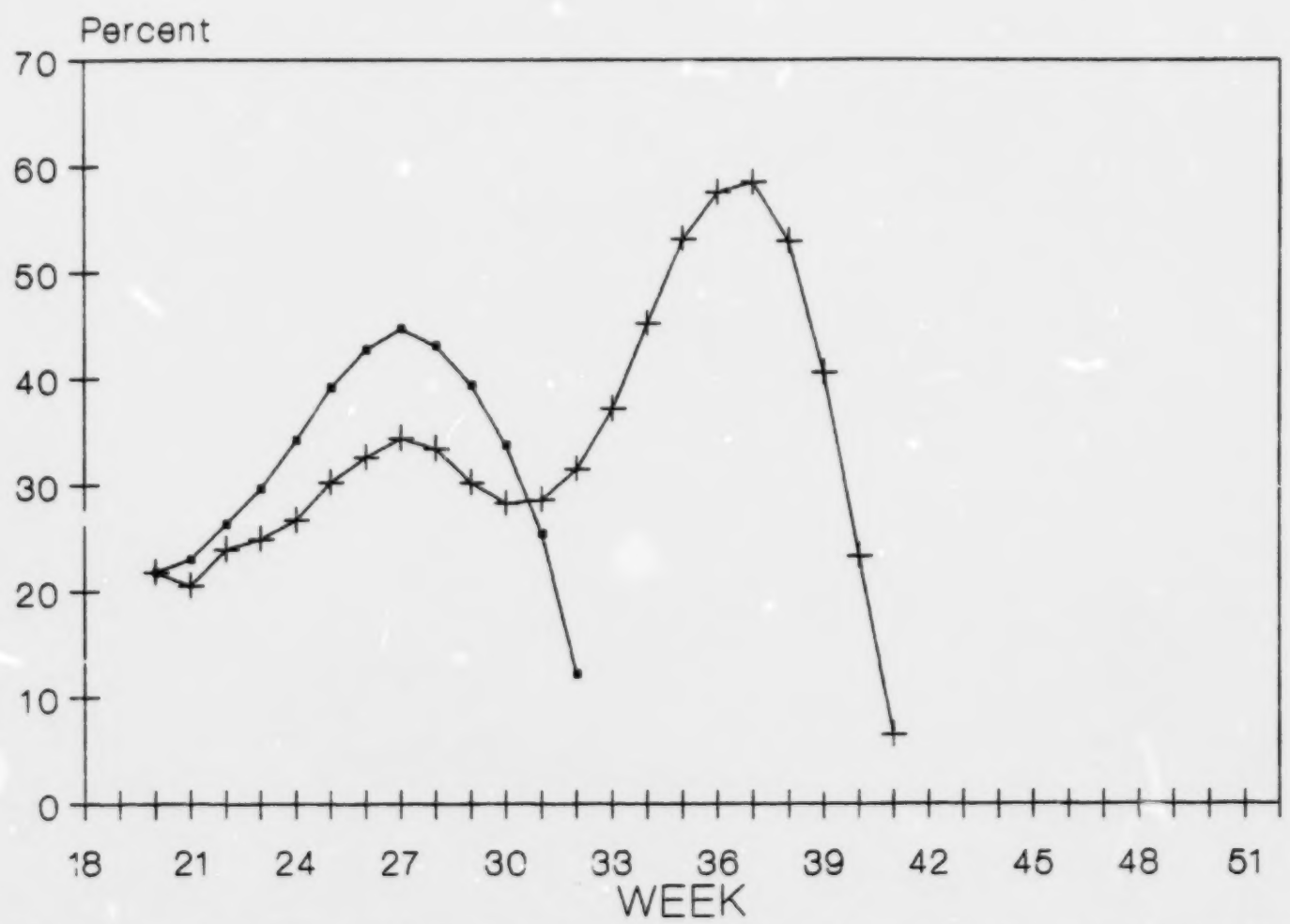

Fig. 16. Percent contribution of chum salmon in even years (when associated with odd brood year pink salmon) to the Hecate Strait juvenile salmon population each week if juveniles follow route 1 (•) or route 5 (+).

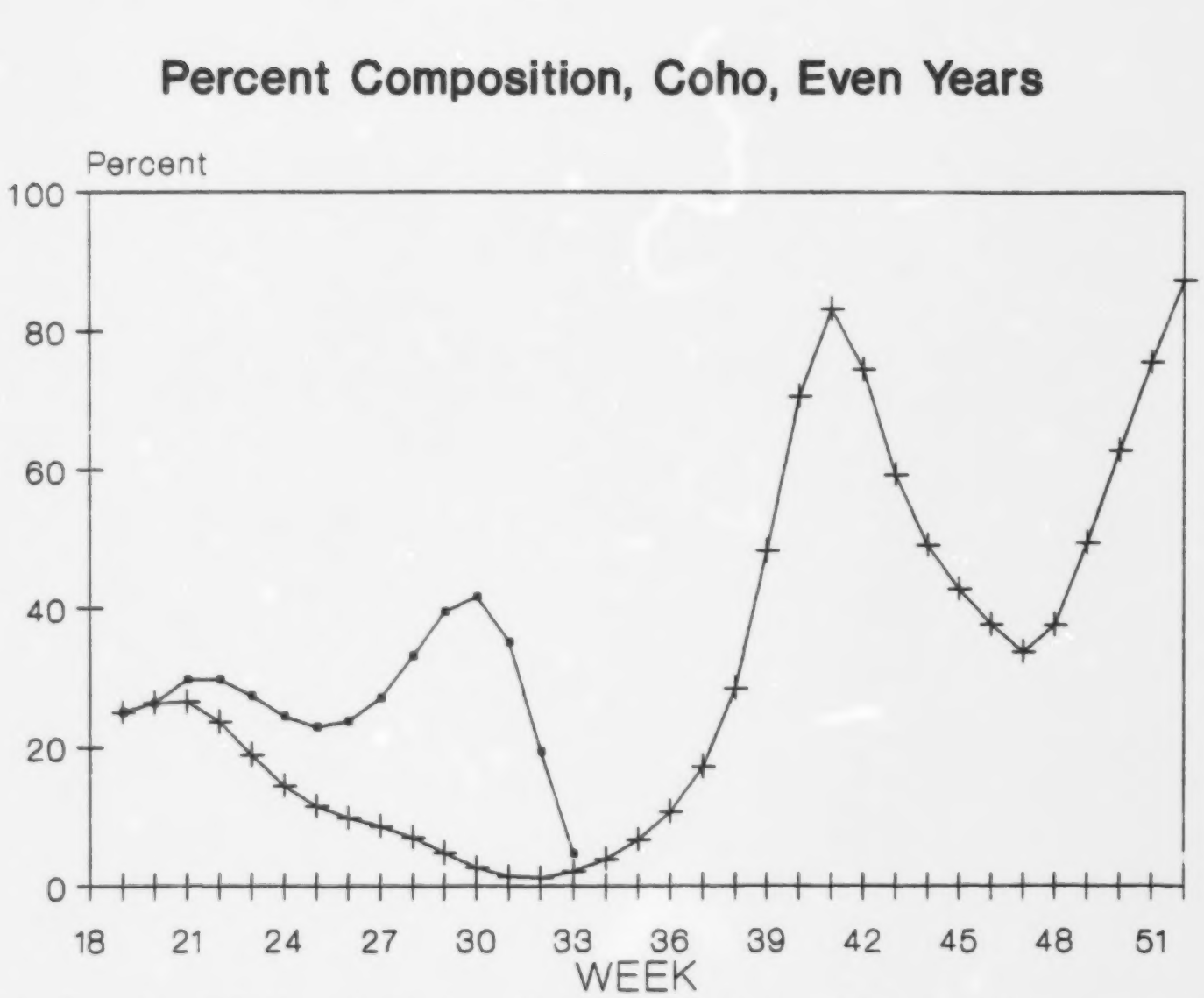

Fig. 17. Percent contribution of coho salmon in even years (when associated with odd brood year pink salmon) to the Hecate Strait juvenile salmon population each week if juveniles follow route 1 (●) or route 5 (+).

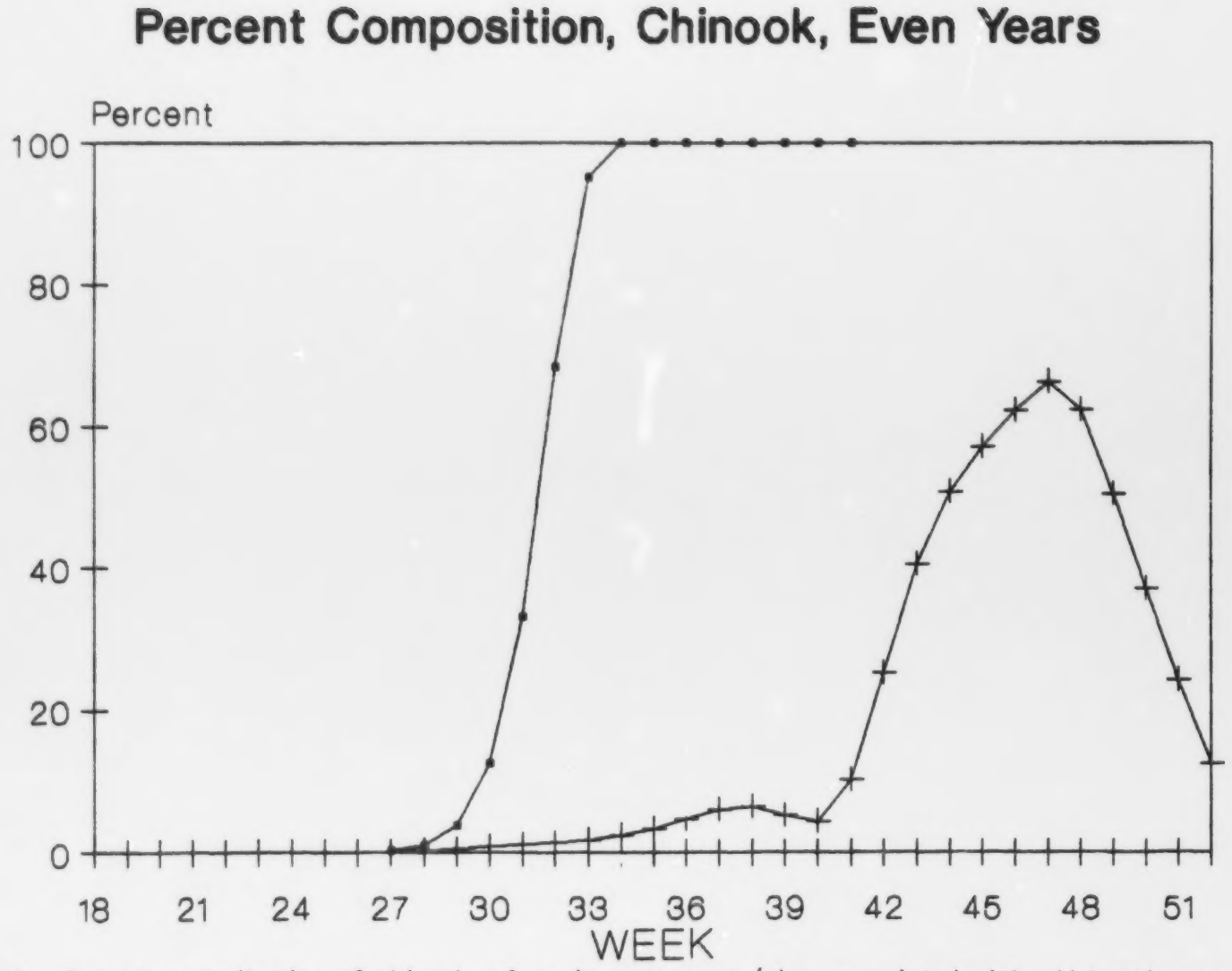

Fig. 18. Percent contribution of chinook salmon in even years (when associated with odd brood year pink salmon) to the Hecate Strait juvenile salmon population each week if juveniles follow route 1 (•) or route 5 (+).

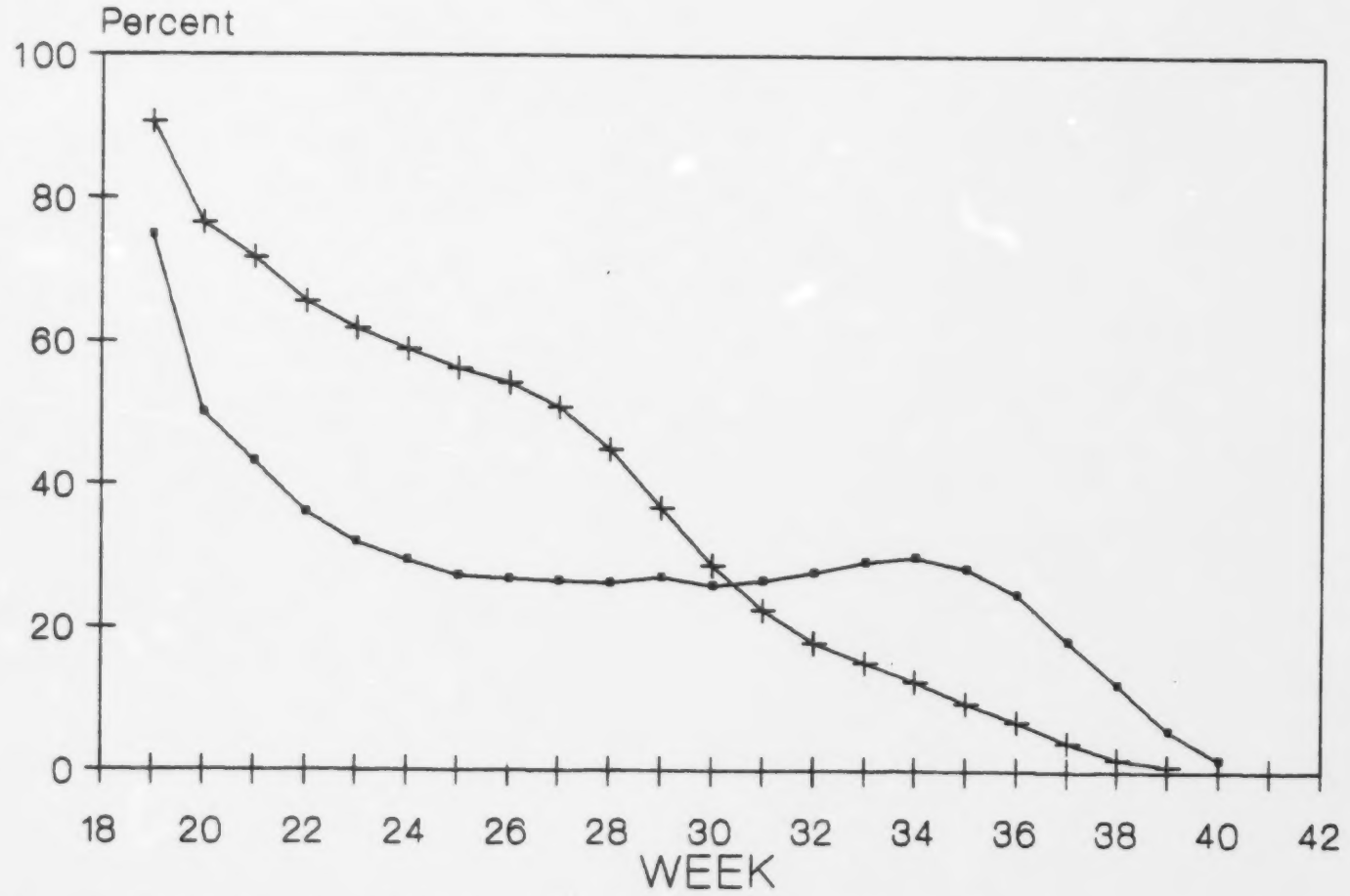

Fig. 19. Percent contribution of odd brood year (■) and even brood year (+) pink salmon to the Hecate Strait population.

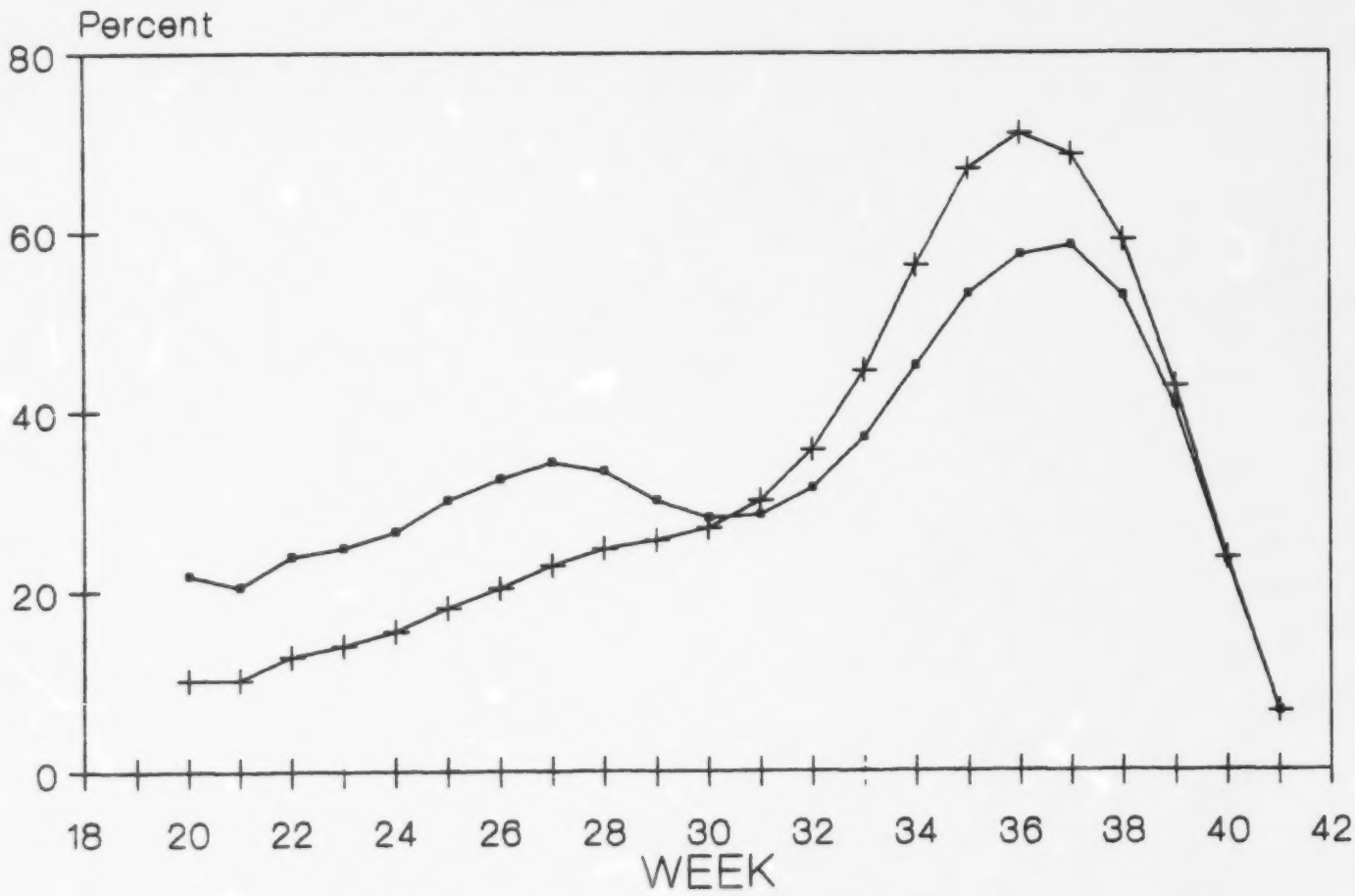

Fig. 20. Percent contribution of chum salmon to the Hecate Strait population when associated with odd brood year (+) and even brood year (▪) pink salmon.

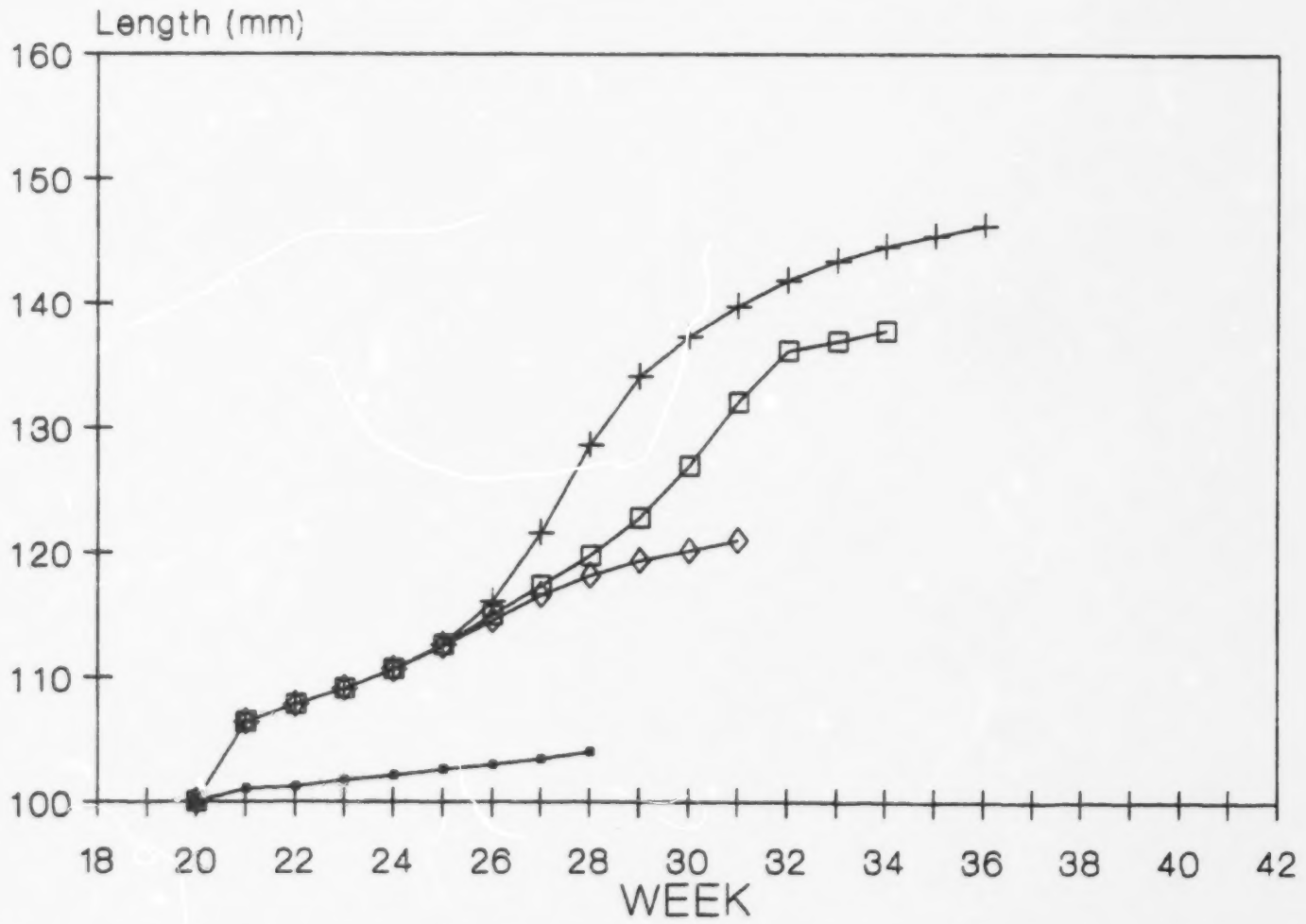

Fig. 21. Average length of sockeye salmon in Hecate Strait each week when the juveniles follow route 1 (●), route 2 (◊), route 3 (□), and route 5 (+). See Table 4 for explanation of routes.

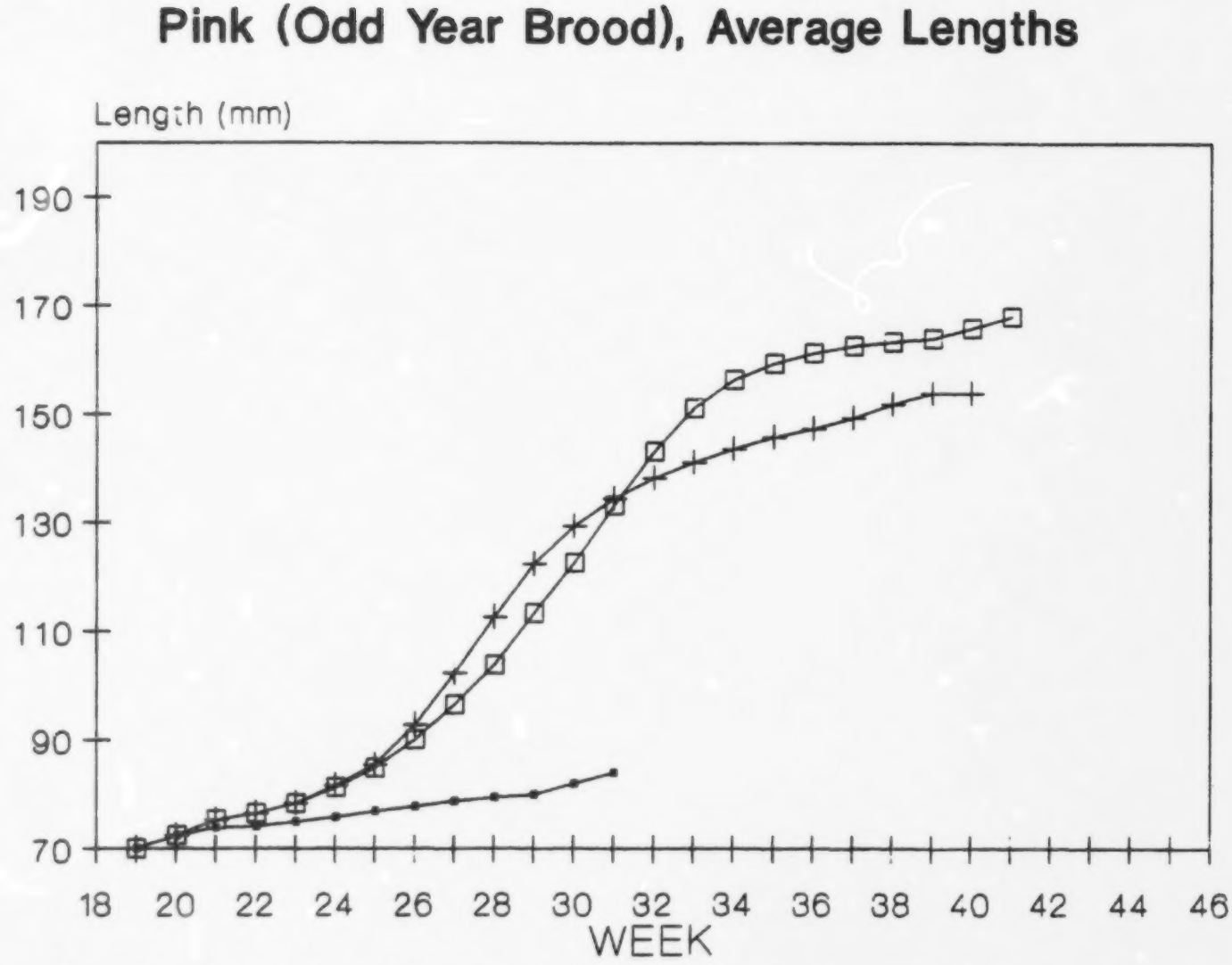

Fig. 22. Average length of odd brood year pink salmon in Hecate Strait each week when the juveniles follow route 1 (•), route 5 (+), and route 6 (□). See Table 4 for explanation of routes.

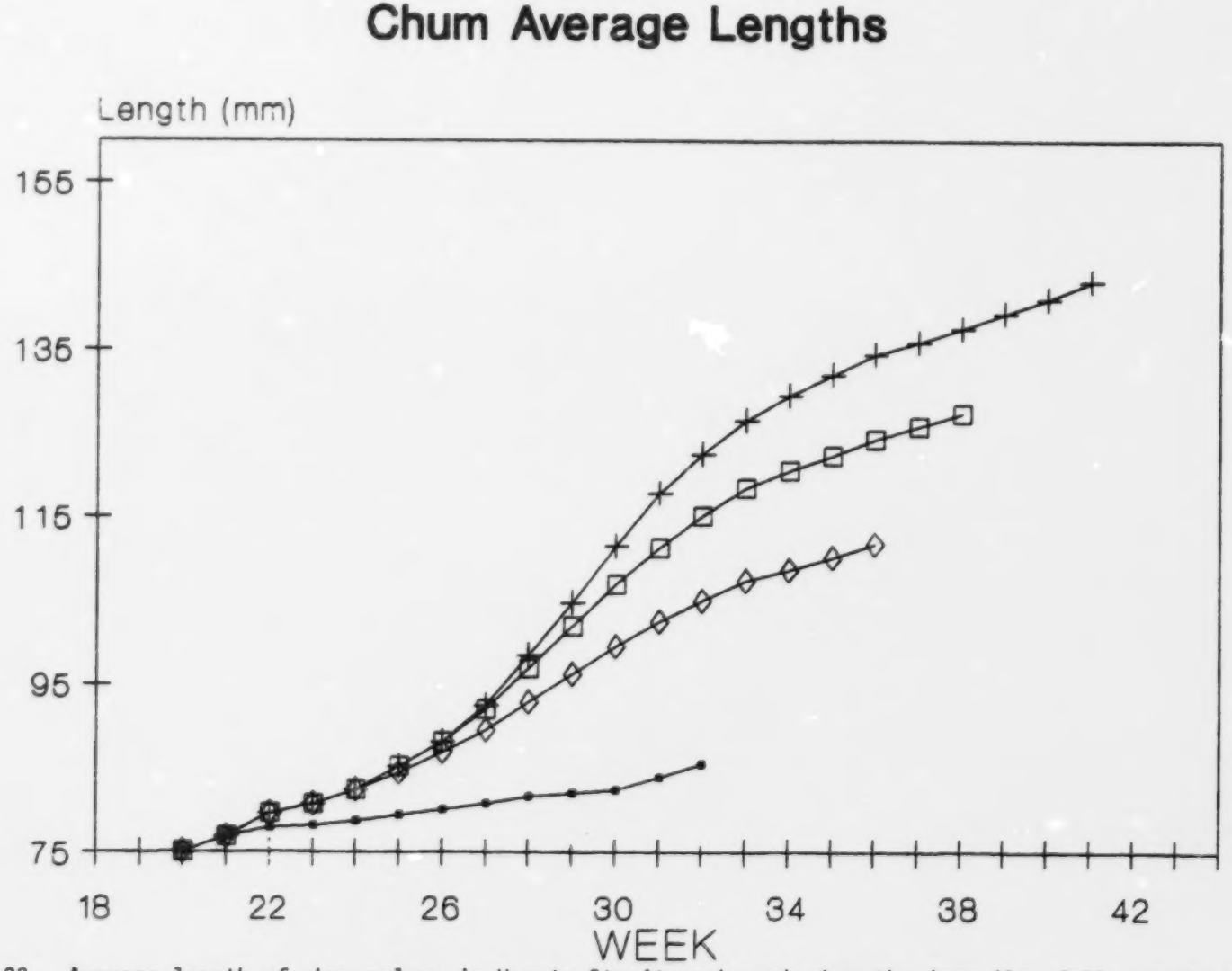

Fig. 23. Average length of chum salmon in Hecate Strait each week when the juveniles follow route 1 (•), route 2 (◊), route 3 (□), and route 5 (+). See Table 4 for explanation of routes.

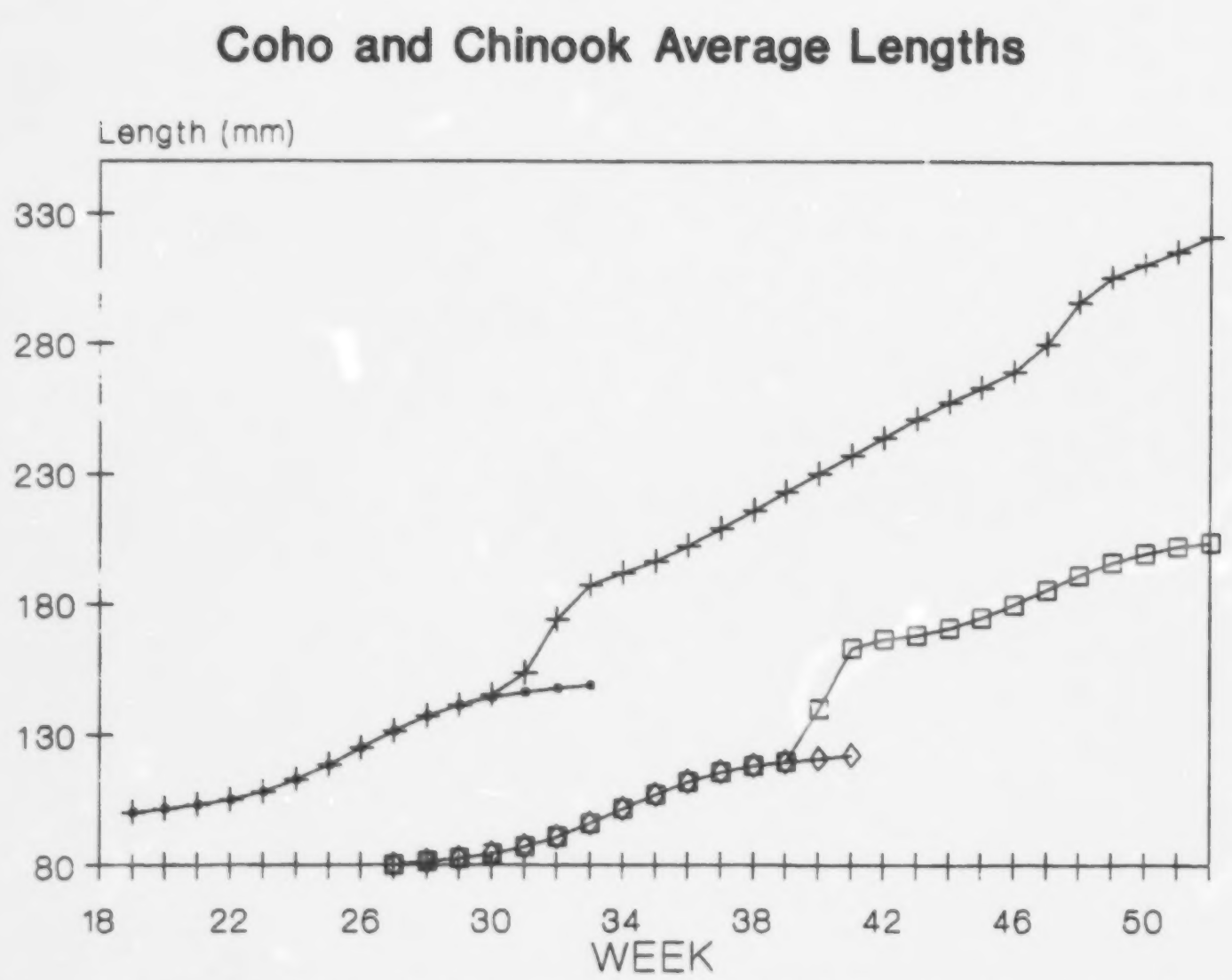

Fig. 24. Average lengths of coho and chinook salmon in Hecate Strait each week when the juveniles follow route 1 (• for coho, ◊ for chinook), and route 5 (+ for coho, □ for chinook). See Table 4 for explanation of routes.

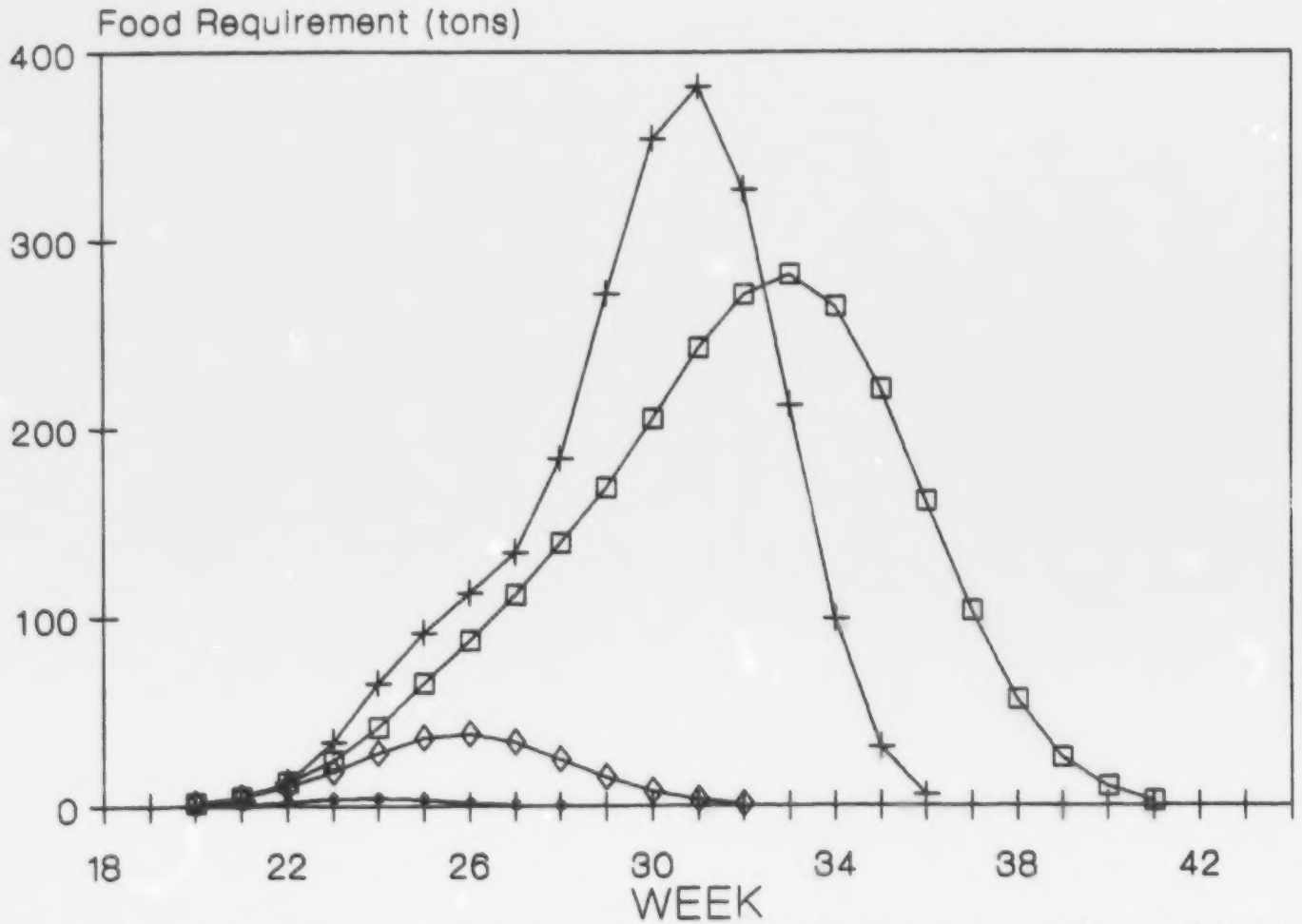

Fig. 25. Food resource demands each week for sockeye salmon following routes 1 (▪) and 5 (+) and chum following routes 1 (◊) and 5 (□).

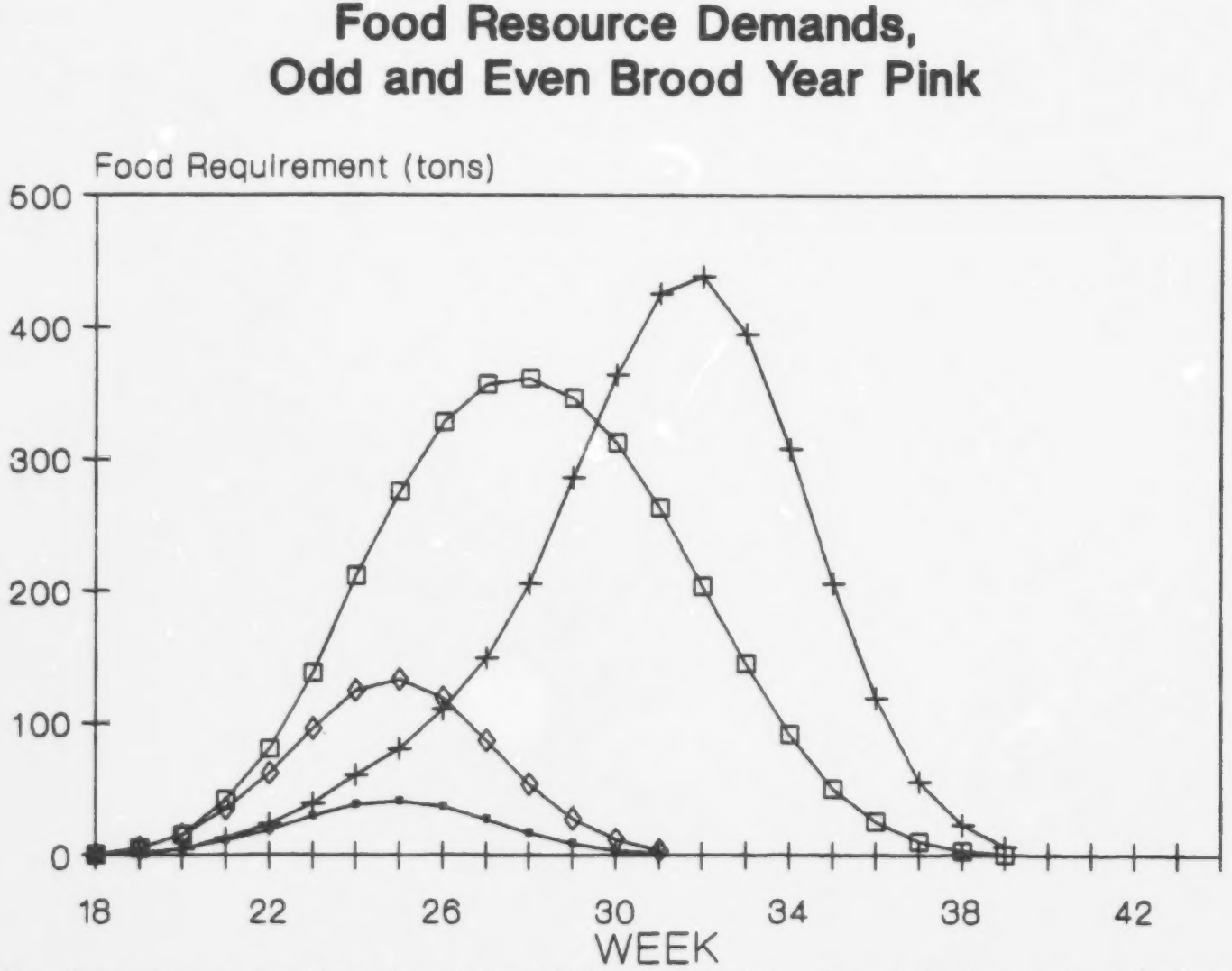

Fig. 26. Food resource demands each week for odd brood year pink salmon following routes 1 (▪) and 5 (+) and even brood year pink following routes 1 (◊) and 5 (◘).

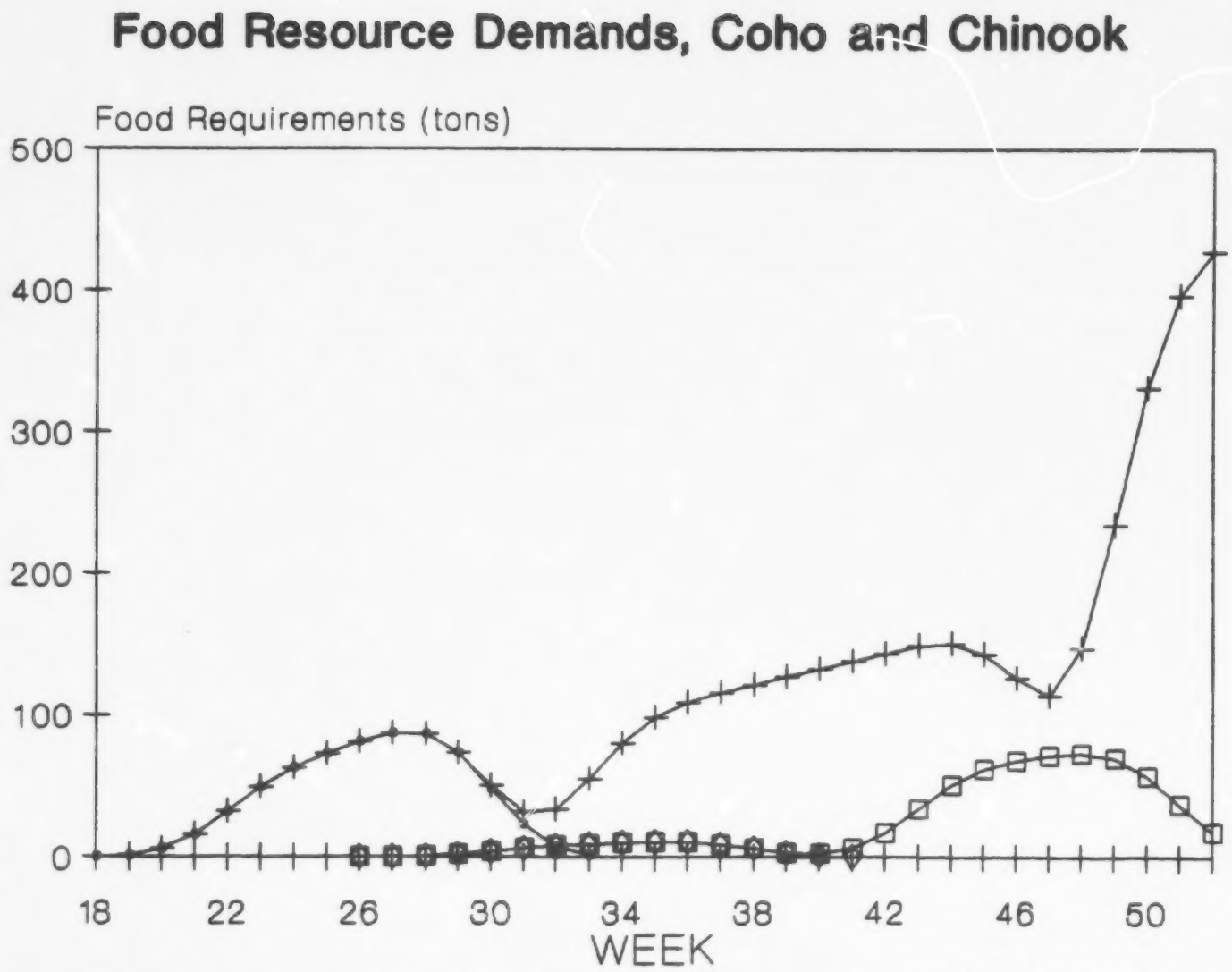

Fig. 27. Food resource demands each week for coho salmon following routes 1 (▪) and 5 (+) and chinook following routes 1 (◊) and 5 (□).

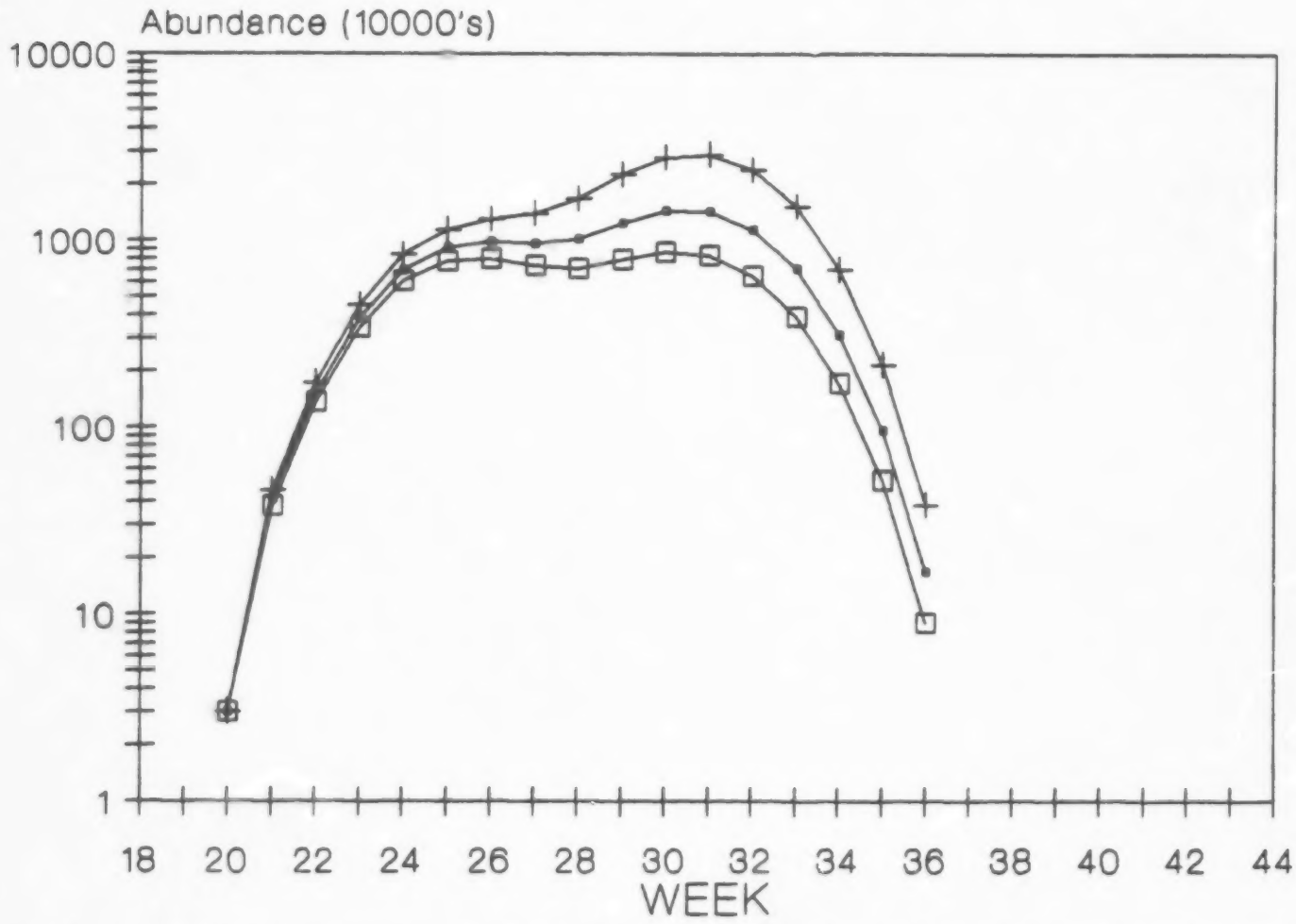

Fig. 28. Abundance of sockeye salmon in Hecate Strait when juveniles follow route 5 and weekly survival is 0.97 (+), 0.90 (■), and 0.85 (□).

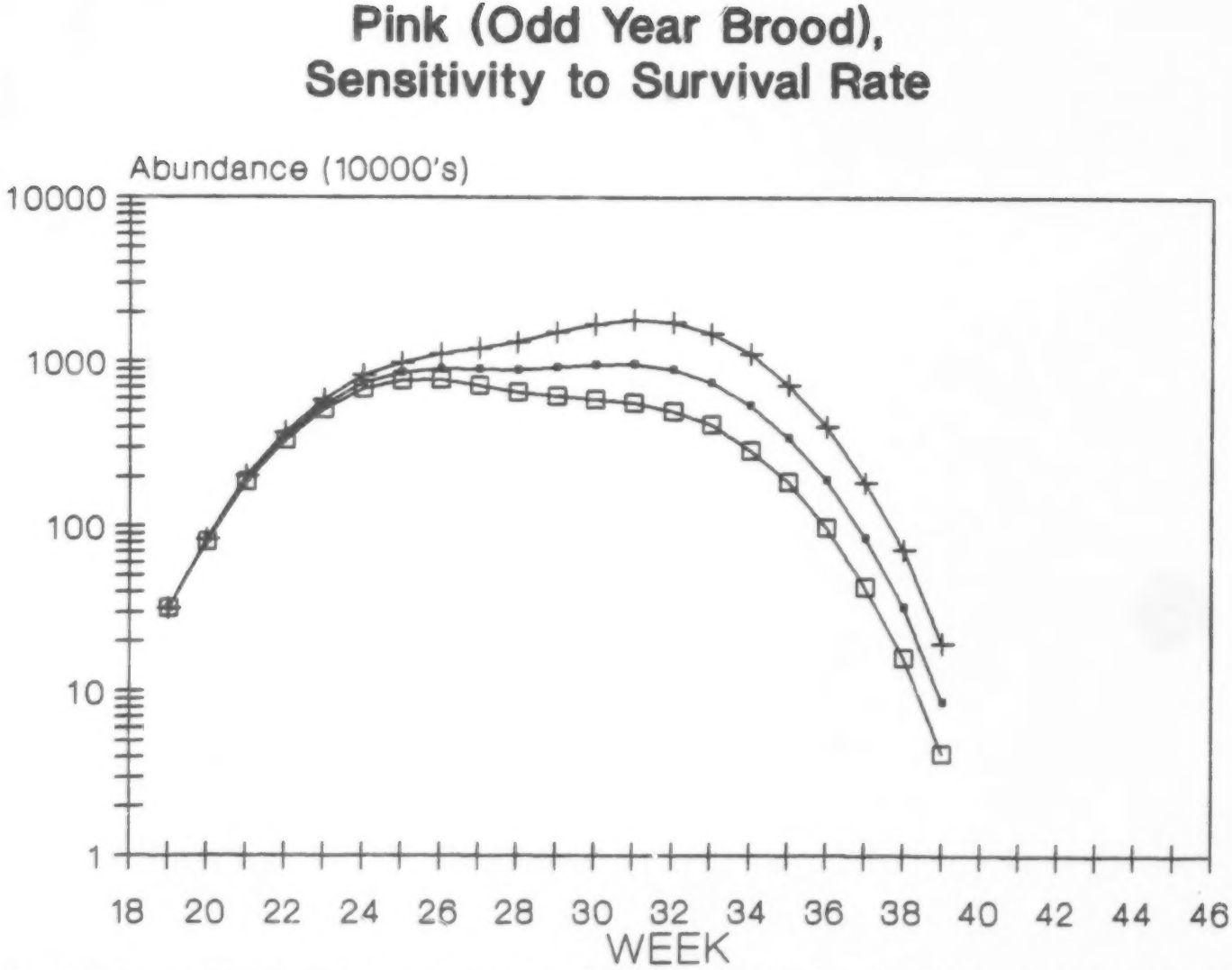

Fig. 29. Abundance of odd brood year pink salmon in Hecate Strait when juveniles follow route 5 and weekly survival is 0.90 (+), 0.85 (▪), and 0.80 (□).

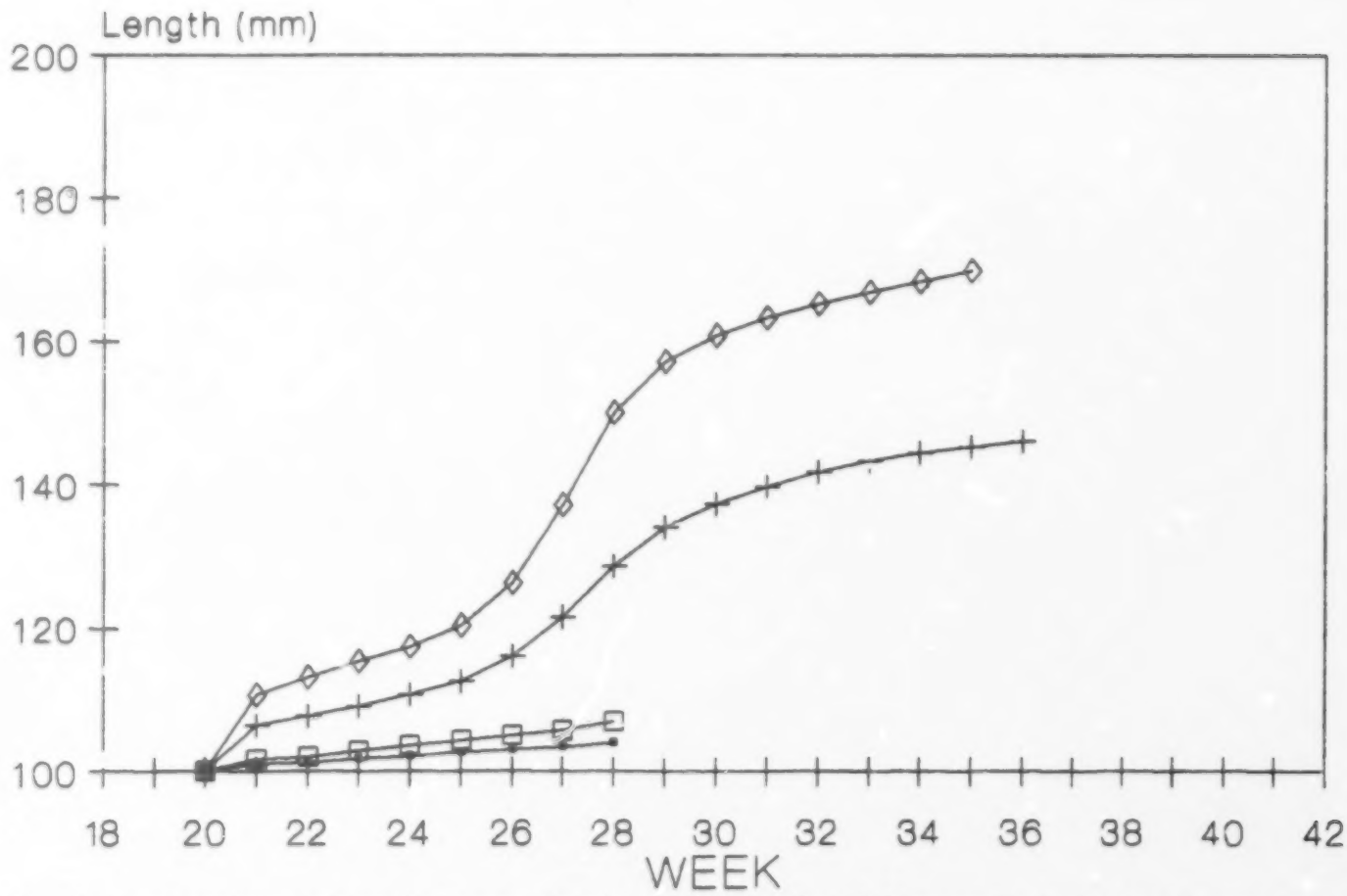

Fig. 30. Size of sockeye salmon in Hecate Strait when juveniles follow route 1 and weekly growth increment is 4.2 mm (■) or 7.0 mm (□), and when juveniles follow route 5 and weekly growth increment is 4.2 mm (+) or 7.0 mm (◊). See Table 4 for explanation of migration routes.

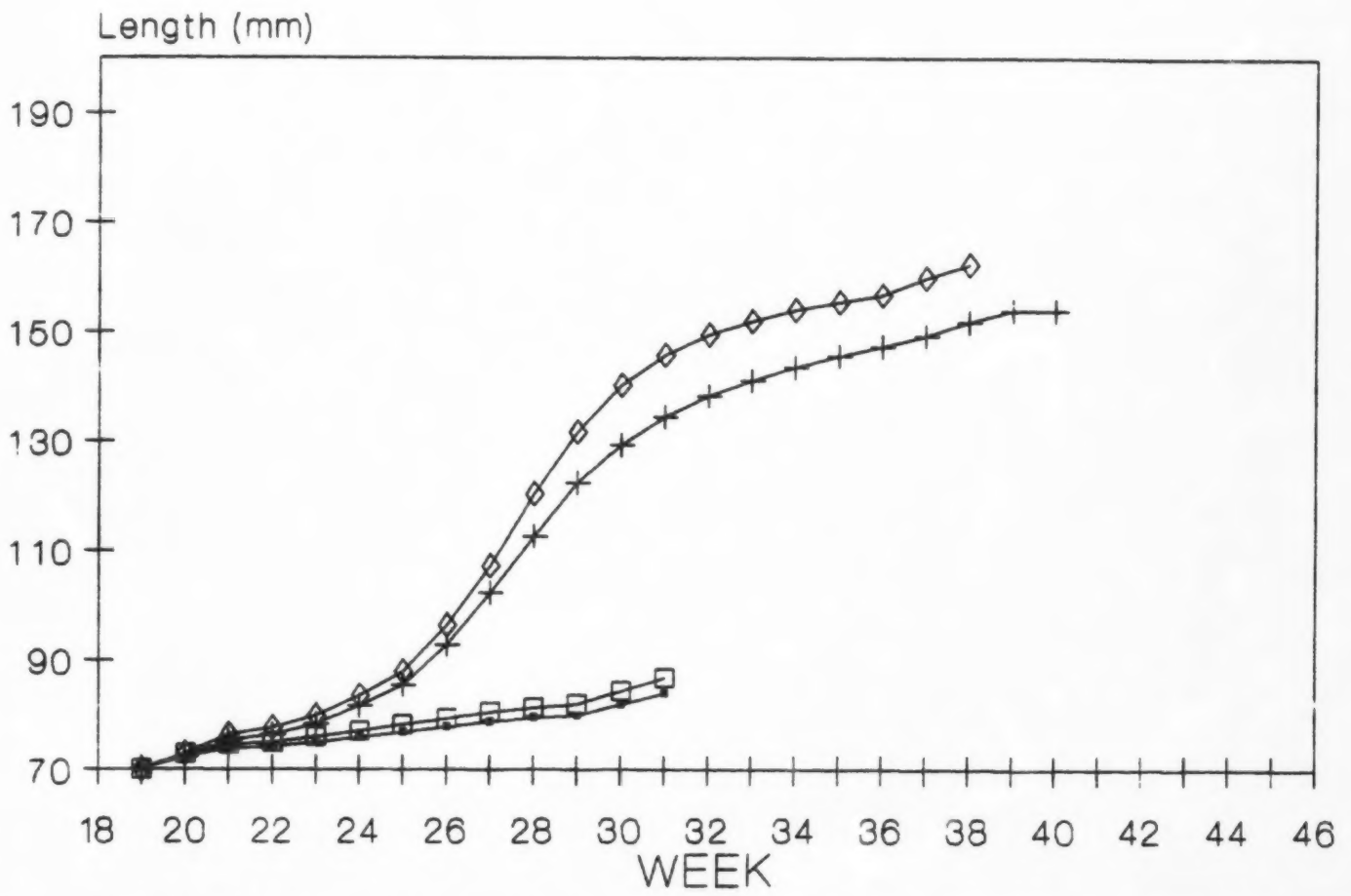

Fig. 31. Size of odd brood year pink salmon in Hecate Strait when juveniles follow route 1 and weekly growth increment is 7.0 mm (▪) or 8.4 mm (□), and when juveniles follow route 5 and weekly growth increment is 7.0 mm (+) or 8.4 mm (◊). See Table 4 for explanation of migration routes.

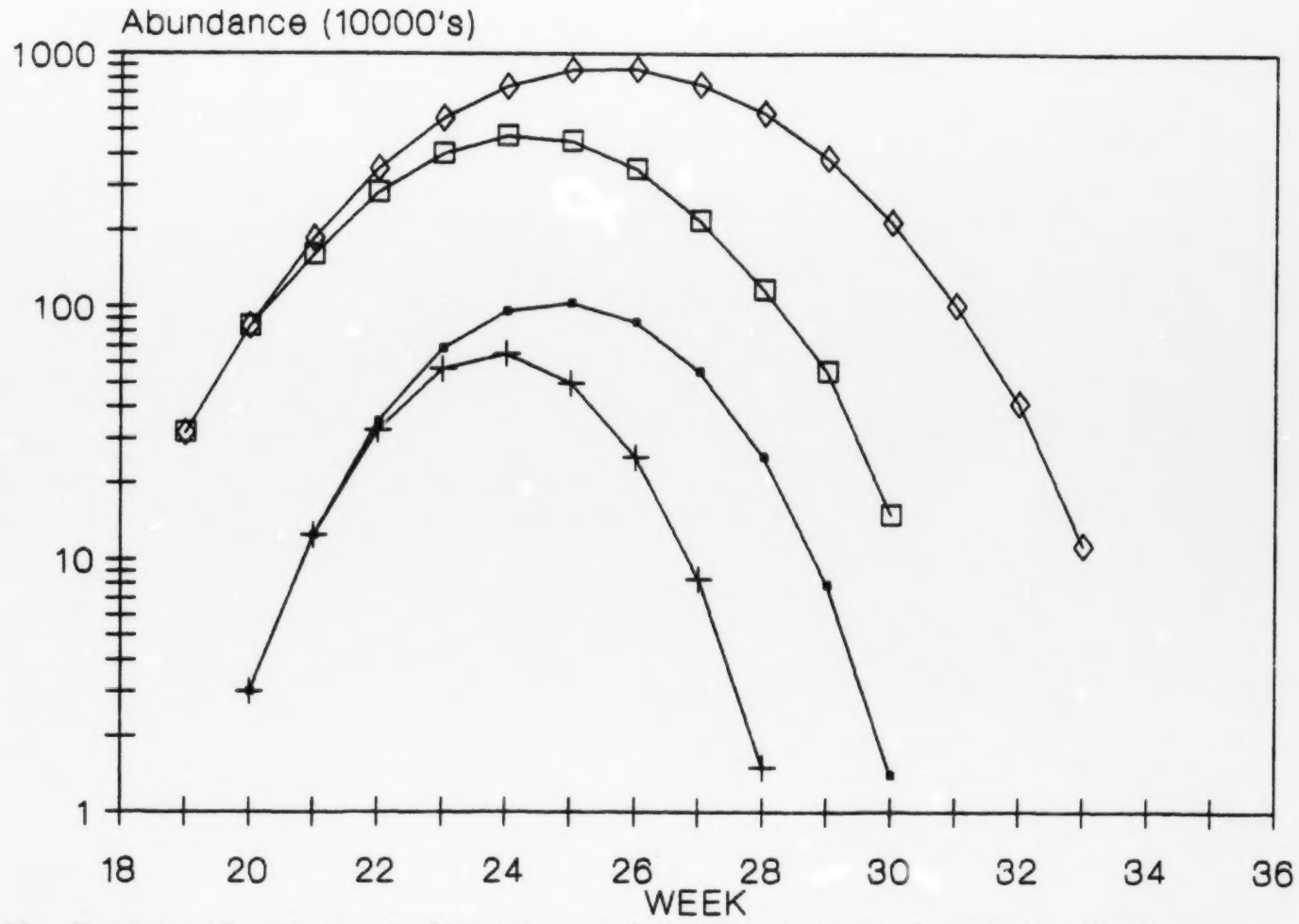

Fig. 32. Abundance of sockeye and odd brood year pink salmon in Hecate Strait when the fish follow route 1 and the migration rate is 0.5 lps (■ for sockeye, □ for pink) or 1.5 lps (+ for sockeye, ◊ for pink).

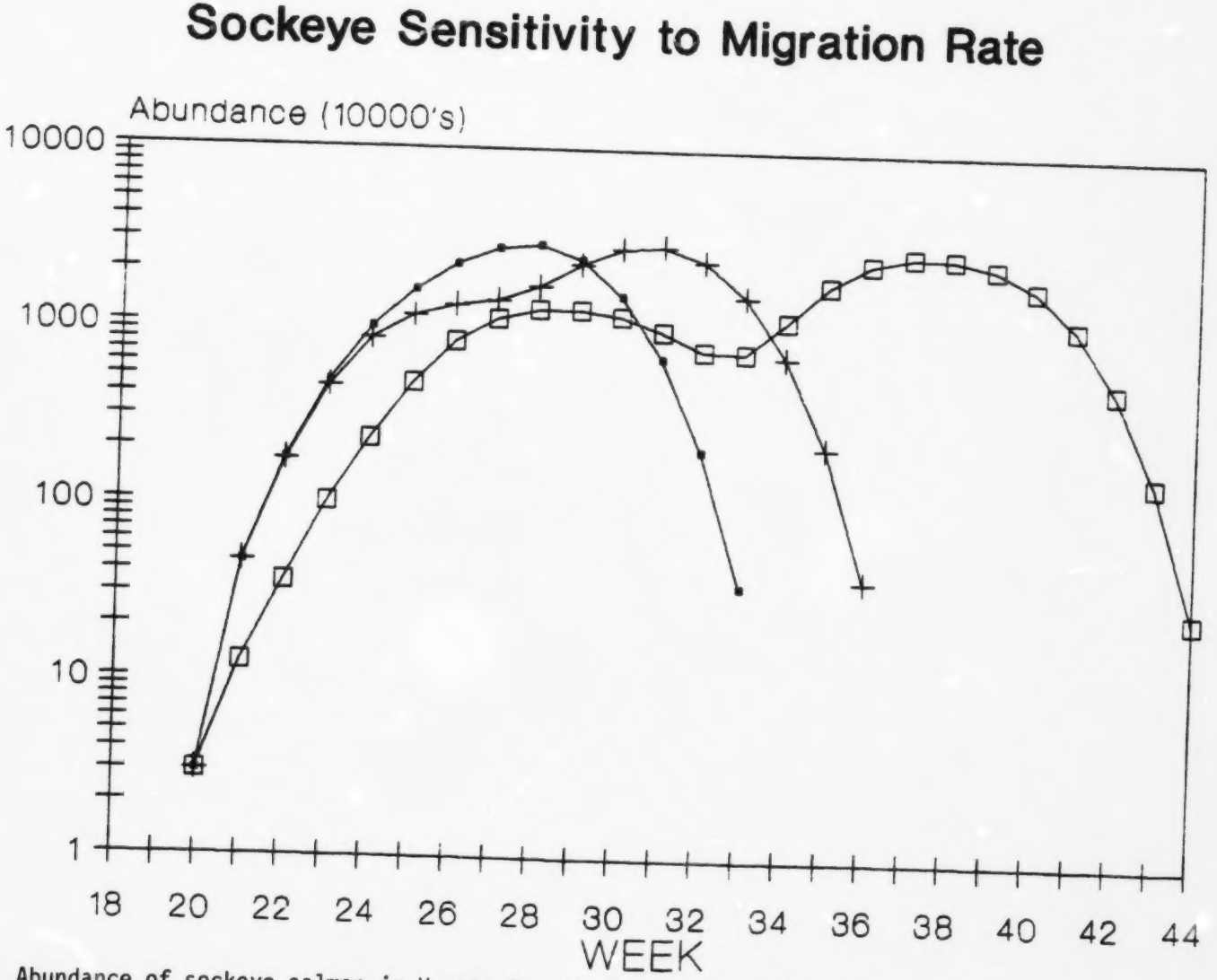

Fig. 33. Abundance of sockeye salmon in Hecate Strait when the fish follow route 5 and their migration route is 0.5 lps (□), 1 lps (+) or 1.5 lps (■).

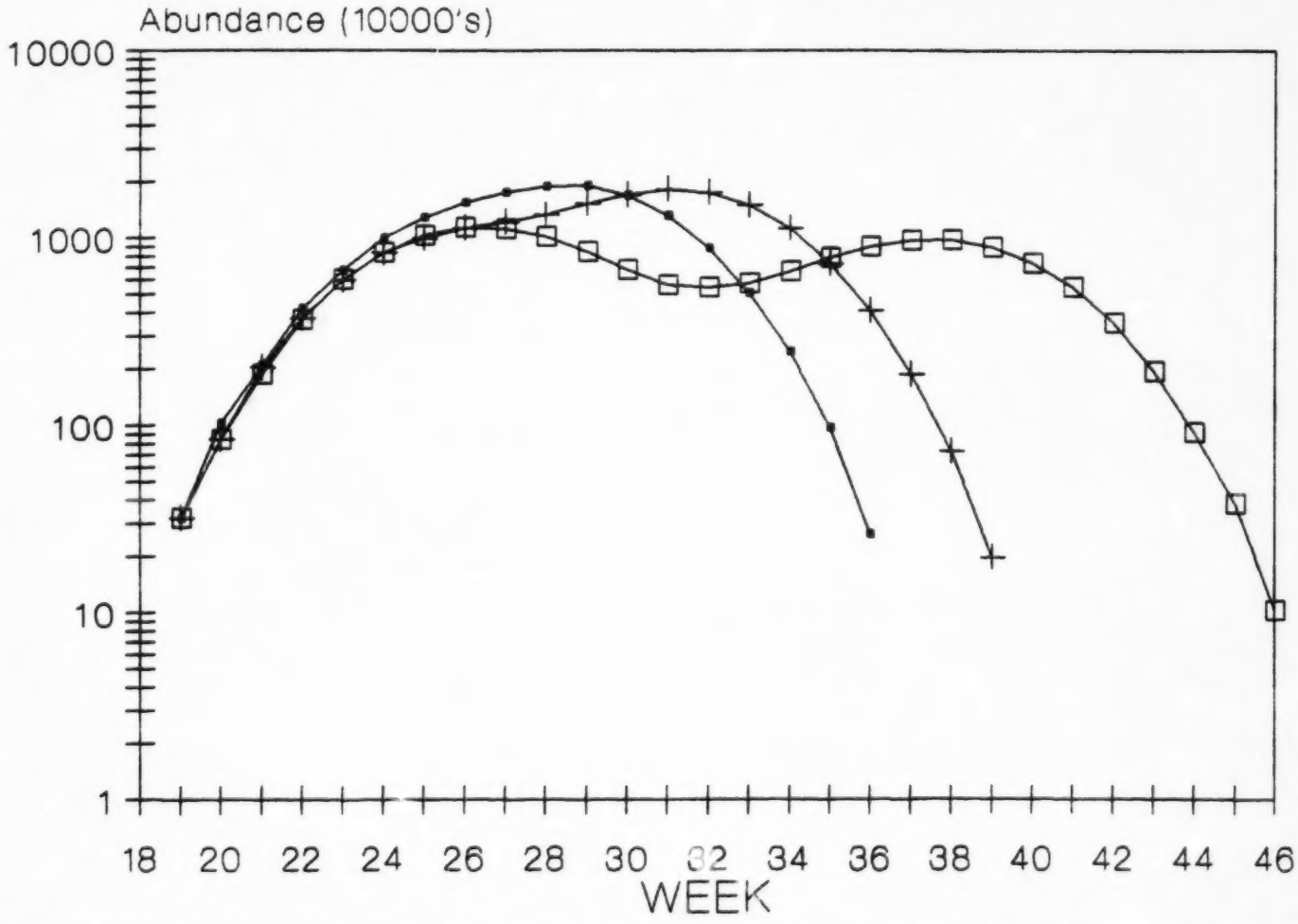

Fig. 34. Abundance of odd brood year pink salmon in Hecate Strait when the fish follow route 5 and their migration rate is 0.5 lps (□), 1 lps (+), or 1.5 lps (■).